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## The Physiology of Polyploidy in Plants

### I. Review of the Literature

G. R. NOGGLE<sup>1</sup>

(Department of Agronomy, University of Illinois, Urbana, Ill.)

Our increasing knowledge of the food values of crops requires an examination of the factors influencing those biochemical activities of plants which are related to the composition of the plant tissues. The effect of increasing the normal number of chromosomes on plant size and on yields of agricultural crops is well known, but the published data have been primarily morphological in nature. It is a matter of considerable interest, therefore, to know how an increase of the number of chromosomes affects the mineral composition, vitamin content, and other nutritive components of plants. With the advent of the colchicine technique and other techniques of increasing the chromosome number, material for biochemical study has become readily accessible.

Various aspects of the physiology of polyploid plants have been reviewed elsewhere. Thus Müntzing (1936) reviewed much of the early work on physiological aspects of polyploidy and discussed the data in relation to evolutionary trends. He distinguished between autopolyploidy, the reduction of the same genome, and allopolyploidy, the summation of different genomes, and concluded that allopolyploidy had played an important part in the evolution of plant species, especially among Angiosperms. In discussing the physiological consequences of autopolyploidy he emphasized the retarding effect which this condition exerted on the growth of the plant.

While reviewing the literature pertaining to the colchicine technique Dermen (1940) mentioned a number of papers dealing with the physiological differences induced by polyploidy. Pirschle (1941) discussed many earlier contributions in relation to his own studies on polyploidy in *Petunia*, and concluded that most of the observed differences between diploids and polyploids could be ascribed to the difference in the rate of growth of the polyploids.

<sup>1</sup> Present address—Blandy Experimental Farm, University of Virginia, Boyce, Va.

Finally Randolph (1941), in a paper describing the value of induced polyploidy as a method of breeding crop plants, reviewed a number of papers describing the physiological differences caused by polyploidy. After discussing the differences which were known to exist, such as a decreased rate of growth, increased water content, and a larger cell size, he emphasized the lack of agreement among authors concerning the nature of the physiological differences due to polyploidy and stated the need for further studies along this line.

#### A. GROWTH

##### I. SIZE OF THE PLANT

One of the common effects of polyploidy is usually an increase in size of the plant parts. Many of the morphological studies on polyploidy have shown a slower rate of growth and development of the polyploid individuals. Pirschle (1941), Schlösser (1940), Shao-Lin Chen and P. S. Tang (1945), and others showed that polyploids grew more slowly than diploids and therefore were about two days to a week behind the diploids in physiological development.

The slower rate of development of the polyploid plants has been thought to depend on a decreased rate of cell division. Wettstein (1924) noted that an altered rate of cell division in the mosses was characteristic of the *gigas* type and Dorries-Rüger (1929) reported similar observations.

The work of several investigators suggests that the slower rate of growth may be caused by the smaller amount of growth hormone present in the tissues. Gustafson (1944) studied two varieties of Marigold (*Tagetes*), Guinea Gold and Golden West, and the cherry tomato (*Lycopersicon pimpinellifolium*). The diploid and the related tetraploids were analyzed at the same stage of development which happened to occur on the same day in his experiment. The autotetraploid marigold, variety Guinea Gold, had only 58.1 per cent as much growth hormone (*Avena* test) as did the diploid; the autotetraploid marigold, variety Golden West, had only 76.3 per cent as much, and the autotetraploid of *L. pimpinellifolium* had only 56.8 per cent as much growth hormone as did the corresponding diploid plants.

Shao-Lin Chen and Tang (1945) investigated the metabolism of colchicine-induced tetraploid barley. The oxygen consumption and carbon dioxide production of germinating seeds of diploid and tetraploid barley were measured by means of Warburg microrespirometers. The tetraploid seeds of barley had a lower rate of respiration than the diploid seeds. These authors thought that the lowered rate of metabolism in the tetraploid seeds may bear a relationship to their slower rate of growth and development.

##### 2. SIZE OF THE CELLS

A number of workers have studied the size of the individual cells of polyploid plants. The Marchals (1909), Winkler (1916), Wettstein (1924),

Sinnott, Houghlating and Blakeslee (1934), and others agree that the volume of the cell is approximately proportional to the chromosome number. However, Kostoff and Axamitnaja (1935a) made a cytogenetical analysis of diploid and autotetraploid tomatoes and of *Petunia* and concluded that the volume of the tetraploid cells usually was not exactly doubled as was the chromatin material; in other words, the chromatin/cytoplasm ratio, and consequently the genes/cell volume ratio, were not alike in the diploid and tetraploid cells. The increase in the cell size of the tetraploids did not lead to an increase of size of the tomato plants but an increase was observed in the size of the plants of tetraploid *Petunia*.

The size of the endosperm cells of tetraploid and diploid corn was studied by Randolph and Hand (1940). They found that the cell volume of the tetraploid cells was about 3.6 times as great as that of the diploid endosperm tissue. Sinnott and Franklin (1943) described a developmental analysis of tetraploid and diploid races of cucurbit fruits and found that the size of both cells and of organ primordia were about twice as great in the tetraploids at the beginning of development. This larger size was maintained until about the time of flowering. However, the diploid plants developed to such an extent between flowering and maturity that at maturity the volume of mature fruit and its constituent cells was alike in both tetraploids and diploids. Randolph, Abbe and Einset (1944), working with diploid and tetraploid maize, compared the tissue of the shoot apex at the time of the initiation of the tenth leaf. They noted no change in the number of cells nor in the cell pattern although the tetraploid cells were larger. The data of these authors may be summarized as follows:

	Shoot apex of maize		Times larger
	Diploid	Tetraploid	
Average cell volume ( $\mu^3$ ) <sup>3</sup>	1,342	2,636	1.96
Nuclear volume ( $\mu^3$ ) <sup>3</sup>	212	421	1.99

### 3. DISCUSSION

There is general agreement among botanists that polyploidy brings about a slower rate of growth. An increase in size of the plants, or of the cells, may or may not be brought about by chromosome doubling. Dermen (1940) considered that the duplication of chromosomes may result in at least three types of tetraploids: "(1) There may occur an appreciable increase in size of each vegetative cell in the tetraploid individual while the total number of cells making up the plant remains relatively the same as in the diploid form; consequently the tetraploid plant appears larger than the diploid individual. Most of the changes following polyploidy appear to fall into this category. (2) An increase in cell volume may follow a doubling of chromosomes but there may be a decrease in the total number of cells making up the tetraploid plant; therefore the tetraploid individual

will not appear different from the diploid. (3) The doubling of chromosomes may not have any effect on the size of the cells. The polyploid individual remains indistinguishable, except probably in sexual and in some obscure physiological behavior." It is apparent that any observable increase in the size of the plant results from an increase in the size of the individual cells which comprise the tissues.

Some of the physiological effects attributed to polyploidy may be related to the changes in the ratio of cell volume to cell surface. Dermen (1940) stated: "It is probable that changes of relationship would occur between total chromosome volume and total chromosome surface, nuclear volume and nuclear surface, and between these and cytoplasmic volume and cell surface. It may therefore be assumed that measurable differences between a diploid and, especially, an autopoloid vegetative sib are expressions of a physiological nature resulting from physical changes of relationship referred to above, rather than of a genetic nature resulting from numerical duplication of genetic factors, e.g., genes." Regarding genetic factors, Dermen wrote, "However, a change in the balance of genes—their activity and genetic expressions—would perhaps result from some physiological consequences of polyploidy which may be in the nature of changes in oxidation and respiration rate, viscosity movement of protoplasm, including cytoplasm and nucleus; in the rate of intake of various substances and output of various metabolic by-products; in enzymatic activities; and a number of other physiological phenomena."

## B. WATER RELATIONSHIPS

### I. WATER CONTENT

A number of investigators have reported data concerning the moisture content of diploid and polyploid plants. It may be assumed that if there is an increase in the moisture content, the osmotic concentration will decrease. Kostoff and Axamitnaja (1935a) calculated that the moisture content of diploid tomatoes was 90.37 per cent while that of tetraploid tomatoes was 91.26 per cent. Fabergé (1936) noticed a higher moisture content in the tetraploid, as compared with diploid, tomatoes. Noguti, Oka and Ôtuka (1940) investigated diploid and tetraploid *Nicotiana rustica* and *N. Tabacum*. The tetraploids had a slightly lower moisture content than the diploids. Pirsche (1941) grew different strains (DD, dd, Dd and DDDD) of *Petunia* in gravel culture and made five cuttings at weekly intervals for chemical analysis. The plant material was separated into leaves and stems. During the early growth, the moisture contents of the diploid and tetraploid leaves and stems were about equal, but as the plants matured, the tetraploid tissue showed the greater percentage of moisture. Schlösser (1937), working with the polyploid tomatoes, *Lycopersicon cerasiforme* and *L. racemigerum*, found a higher moisture content in the

tetraploid forms. Shao-Lin Chen and Tang (1945) found that tetraploid barley seeds contained 5.3 per cent moisture while the diploid seeds contained 5.7 per cent moisture.

## 2. OSMOTIC CONCENTRATION

It was stated above that one of the consequences of polyploidy frequently is an increase in cell size and an increase in the moisture content, with a consequent decrease in the osmotic pressure. Becker (1931) reported that his studies of the relationship between the chromosome number and osmotic pressure in moss species showed that the osmotic pressure was inversely proportional to the chromosome number. With *Physcomitrium piriforme*, he found that the osmotic pressure decreased from  $12.15 \pm 0.158$  atmospheres for the univalent series to  $9.759 \pm 0.116$  atmospheres for the tetravalent series. Schlösse (1936), in a study on the relation between frost hardness and polyploidy, determined the osmotic value of the expressed juice of winter rape. The osmotic concentration was equivalent to 0.71 mol. of sugar in the 2N plants, and only 0.48 in the 4N plants. Schlösse (1937) later reported that the osmotic concentration of 2N wild tomatoes was equivalent to 0.63—0.60 mol. but only 0.46—0.47 mol. for 4N plants.

Hesse (1938), in an investigation with *Petunia*, noted that the water content of tetraploids was somewhat higher, and that the osmotic concentration was a little lower in the tetraploids. Gries (1940) measured the osmotic concentrations of diploid and tetraploid barley and found that the leaf cells of the 2N plants showed an osmotic concentration equivalent to  $0.516 \pm 0.006$  mol. of sugar, while the concentration in 4N plants was  $0.346 \pm 0.01$ . A barley chimera with diploid and tetraploid stalks was also investigated, the 2N tissue exhibited an osmotic concentration of  $0.517 \pm 0.01$  mol., while that of 4N tissue was  $0.344 \pm 0.004$  mol. Pirschle (1941) mentions some unpublished work by Györffy, who investigated the osmotic concentration of *Petunia*, *Solanum*, *Capsicum*, and other polyploid plants. Györffy found only small differences, and in some cases even higher osmotic concentrations in the polyploid tissue at various stages of development. Taylor (1942) found the osmotic concentration to be considerably reduced in tetraploid *Vinca*, but found small differences between diploid and tetraploid *Petunia*. Freisleben (1942) produced tetraploid barley by heat shock at the time of the first division of the zygote, and studied the water relationships of the plants. He found the osmotic concentration of the cell sap of the tetraploid plants to be lower than that of the diploids. Oka (1942) induced tetraploidy in five varieties of tomatoes by the decapitation-callus method. The cell sap concentration decreased 0.06—0.14 mol. in the root hairs and 0.2 mol. in the leaves of the tetraploids. Shao-Lin Chen and Tang (1945) found that the osmotic value of the cell

sap of diploid barley was equivalent to 0.9 M of sucrose solution while the cell sap of tetraploid barley was equivalent to 1.1 M of sucrose solution. They also investigated the suction pressure of the leaves of diploid and tetraploid barley. The diploid leaves had a suction pressure equivalent to 0.75 M of sucrose solution while the tetraploid leaves had a suction pressure equivalent to 0.875 M of sucrose solution.

### 3. TRANSPERSION, IMBIBITION

Shao-Lin Chen and Tang (1945) measured the rates of transpiration of 55-day old diploid and tetraploid barley by means of potometers. The diploid seedlings transpired 78.3 ml. of water per gram of dry weight while the tetraploid seedlings transpired 38.8 ml. of water per gram of dry weight. The same workers studied the imbibition of water by seeds of diploid and tetraploid barley and noted that the tetraploid seeds had a higher imbibition capacity.

### 4. DISCUSSION

The majority of the experimental evidence indicates that polyploid plants have a higher water content than diploids. Most of the samples have been obtained at only one stage in the development of the plant, but it is well known that the moisture content of tissue changes with the age of the plant. Before any general statement could be made regarding the moisture content, studies should be made on plants at various stages of growth.

The question of cell size is intimately related to the problem of osmotic pressure, moisture content, and the chemical composition of polyploid plants. With an increase in cell size, there is an increase in the amount of cell sap, and there may or may not be a decrease in the concentration of its soluble constituents. Also, a decrease may occur in the percentage of structural constituents such as cellulose and crude fiber.

Most investigators are in agreement that the osmotic concentration of polyploid forms is lower than in diploids. This condition probably is due to the fact that the polyploid forms have the higher moisture content, and the osmotic concentration is consequently reduced.

The published data on water content and the osmotic concentration are summarized in the following table (Table 1).

## C. COMPOSITION

### I. ORGANIC COMPONENTS

#### a. Nitrogen fractions

*1. Total nitrogen.*—Heilbronn (1933) found that the diploid fronds of *Polypodium aureum* contained 0.578 per cent nitrogen and the tetraploid fronds 0.568 per cent, calculated on the fresh weight basis. Kostoff and

Axamitnaja (1935) in a study of  $F_1$  hybrids of *Nicotiana* and their amphidiploids, found that the  $F_1$  hybrid of *N. rustica*  $\times$  *N. paniculata* contained 6.01 per cent total nitrogen while the amphidiploid contained only 2.74 per cent. The  $F_1$  hybrid *N. glauca*  $\times$  *N. Langsdorffii* contained 5.16 per cent total nitrogen, while the amphidiploid contained 5.31 per cent. Kostoff and Axamitnaja (1935a) determined that *S. Lycopersicum* tetraploids contained a higher percentage of total nitrogen than the diploids, while the

TABLE I. Summary of the data concerning the water content and the osmotic concentration of diploid and tetraploid plants.

	Osmotic concentration		Water content	
	Diploid	Tetraploid	Diploid	Tetraploid
<i>Physcomitrium piriforme</i>	higher	—	—	—
Winter rape	higher	—	—	—
Wild tomato	higher	—	—	—
<i>Petunia</i>	higher	—	—	higher
Barley	higher	—	—	—
<i>Petunia</i>	little difference	—	—	—
<i>Solanum</i>	little difference	—	—	—
<i>Capsicum</i>	little difference	—	—	—
<i>Vinca</i>	higher	—	—	—
<i>Petunia</i>	no difference	—	—	—
Barley	higher	—	—	—
Tomato	higher	—	—	—
Tomato	—	—	—	higher
Tomato	—	—	—	higher
<i>Nicotiana</i>	—	—	higher	—
<i>Petunia</i>	—	—	—	higher
Tomato	—	—	—	higher
Barley seeds	—	—	higher	—
Barley	—	higher	—	—

*Petunia* diploids and tetraploids contained about the same percentage of nitrogen.

Sullivan and Myers (1939), by an experimental treatment of the seeds of *Lolium perenne* L., obtained plants which were chimeras of diploid and tetraploid tissue. These were vegetatively propagated and a number of diploid and tetraploid clones were established. The arithmetical mean of the percentage of total nitrogen in ten such diploid and tetraploid clones was 4.762 for the diploids and 4.647 for the tetraploids, calculated on the dry weight basis. Noguti, Oka and Ôtuka (1940) found a higher percentage of total nitrogen in all tetraploid samples of *Nicotiana Tabacum* var. Yellow Orinoco. In his study of polyploid barley, Gries (1940) noted that the

diploid plants contained 2.10 per cent nitrogen and the tetraploid 1.12 per cent, calculated on a dry weight basis. Schlösse (1940) found the nitrogen content of diploid and tetraploid tomato shoots to be approximately identical, while in the roots of the tetraploids, the nitrogen content was smaller. In a series of analyses on the leaves of polyploid sugar beets, the diploid forms were found to contain 2.24 per cent, the triploid 1.76 per cent, and the tetraploid 1.56 per cent. Pirschle (1941) did not find much difference in the percentage of nitrogen in diploid and tetraploid *Petunia*; although in most cases, the tetraploid values were slightly higher, he believed the differences to fall within the range of his experimental error.

Sullivan (1944) grew diploid and tetraploid rye grass under field conditions and analyzed the tops for the percentage of total nitrogen. He reported no difference between the diploids and the tetraploids. Sullivan also grew rye grass in gravel culture in low-nitrate and high-nitrate nutrient solutions. Different frequencies of clipping were made and the tops analyzed. There was little difference in the total nitrogen. The same investigator grew tetraploid and octoploid *Trifolium repens* under field conditions and again the percentage of total nitrogen did not differ significantly in the two strains. Shao-Lin Chen and Tang (1945) analyzed the seeds of diploid and tetraploid barley and found that the diploid seeds contained 12.7 per cent protein while the tetraploid seeds contained 14.7 per cent protein.

2. *Protein and colloidal nitrogen*.—Kostoff and Axamitnaja (1935), in a study of F<sub>1</sub> hybrids of *Nicotiana* and their amphidiploids, determined protein nitrogen. The F<sub>1</sub> hybrid of *N. rustica* × *N. paniculata* contained 5.61 per cent protein nitrogen and 35.00 per cent protein (protein N × 6.25), while the amphidiploid contained 2.48 per cent protein nitrogen and 15.90 per cent protein. The F<sub>1</sub> hybrid *N. glauca* × *N. Langsdorffii* contained 5.09 per cent protein nitrogen and 31.81 per cent protein with the amphidiploid containing 4.50 per cent protein nitrogen and 28.12 per cent protein.

Protein nitrogen and protein were determined in diploid and tetraploid tomatoes and *Petunia* by Kostoff and Axamitnaja (1935a). *S. Lycopersicum* tetraploids were found to contain more protein nitrogen and protein than the diploids. The *Petunia* diploids contained more protein nitrogen and protein than the tetraploids. Sullivan and Myers (1939), by treatment of seeds of *Lolium perenne* L., obtained plants which were chimeras of diploid and tetraploid tissue. Following vegetative propagation, a number of diploid and tetraploid clones were established. The arithmetical mean of ten such diploid and tetraploid clones gave the following data: alcohol insoluble nitrogen (colloidal nitrogen) 2N = 3.516 per cent, 4N = 3.466 per cent. Barr and Newcomer (1943) studied colloidal nitrogen in diploid and tetraploid cabbage and found that the diploid plants contained less colloidal nitrogen than the tetraploids. Sullivan (1944) grew diploid and tetraploid rye grass under field conditions and analyzed the tops for insoluble

or colloidal nitrogen. He reported no differences between the amount of protein nitrogen in the diploid and tetraploid plants. Rye grass grown in gravel culture in a low-nitrate and a high-nitrate nutrient solution and clipped with different frequencies, were analyzed, but there was little difference in the insoluble nitrogen produced by these treatments.

3. *Soluble nitrogen*.—Sullivan and Myers (1939) established clones of diploid and tetraploid *Lolium perenne* L., and studied the amounts of soluble nitrogen in the two types. The arithmetical means of ten such diploid and tetraploid clones showed that the diploids contained 1.241 per cent of alcohol-soluble nitrogen and the tetraploids 1.174 per cent. Barr and Newcomer (1943) studied soluble nitrogen in diploid and tetraploid cabbage and discovered that the diploid plants contained more soluble nitrogen than the tetraploids. Sullivan, in a study of field grown rye grass, analyzed the tops and reported no difference in soluble nitrogen between the diploids and tetraploids. He also grew rye grass in gravel culture in low-nitrate and high-nitrate nutrient solutions. Different frequencies of clipping were made and the tops analyzed. There was little difference in the percentage of soluble nitrogen produced by the various treatments.

4. *Discussion*.—Most of the published data indicate that the diploid plants contain a higher percentage of nitrogen. None of the investigators suggested any particular reason why the tetraploid plants should contain less nitrogen. The experimental work also shows that the diploid plants contain more protein nitrogen than the polyploids. Barr and Newcomer (1943) found that diploid plants contained less protein nitrogen and more soluble nitrogen. The authors suggested that the higher soluble nitrogen content of the diploid plants might be explained by assuming that soluble nitrogen was utilized in synthesizing the 4N protoplast, thereby causing a higher colloidal or protein nitrogen percentage in the tetraploid tissue.

The data regarding the nitrogen content of diploid and polyploid plants are summarized in Table 2.

#### b. Carbohydrate components

1. *Starch*.—Heilbronn (1928) noted that the production of starch was much greater in the fronds of tetraploid *Polypodium aureum* than in the diploid fronds. Kostoff and Axamitnaja (1935a) could find little difference in the starch content of diploid and tetraploid *Petunia*. Diploid tomatoes contained more starch than tetraploid plants. Kostoff and Axamitnaja (1935) reported that the amphidiploids of F<sub>1</sub> hybrids of *Nicotiana* had a higher starch content. According to Barr and Newcomer (1943) tetraploid cabbage contained more starch than did the diploid plants.

2. *Cellulose*.—Kostoff and Axamitnaja (1935) found that F<sub>1</sub> hybrids of *Nicotiana* contained slightly higher amounts of cellulose than did their amphidiploids. The same authors (1935a) could find little difference in the

cellulose content of diploid and tetraploid *Petunia*. There was little difference in the cellulose content of diploid and tetraploid tomatoes.

3. *Hemicellulose*.—Similarly Kostoff and Axamitnaja (1935) found that the F<sub>1</sub> hybrids of *Nicotiana* contained slightly higher percentages of hemicellulose than their corresponding amphidiploids. According to these authors (1935a) there is little difference in the hemicellulose content of

TABLE 2. Summary of the published data concerning the percentage of nitrogen in diploid and tetraploid plants; x signifies an increase; — signifies no difference.

Species	Total Nitrogen		Protein and Colloidal Nitrogen		Soluble Nitrogen	
	Diploid	Polyploid	Diploid	Polyploid	Diploid	Polyploid
<i>Polyplodium aureum</i>	x					
<i>Nicotiana</i>	x			x		
<i>Nicotiana</i>		x		x		
<i>Nicotiana</i>		x				
<i>Petunia</i>			x			
<i>Petunia</i>	—	—	x			
Tomato		x	x	x	x	
Tomato roots	x					
<i>Lolium perenne</i>	x		x		x	
<i>Lolium perenne</i> (field)	—	—	—	—	—	—
Barley	x					
Sugar Beets	x					
Cabbage					x	x
Barley	x					

diploid and tetraploid *Petunia*, although tetraploid tomatoes contained more hemicellulose than the diploid plants.

4. *Total sugars*.—Oka (1940) noted an increase in the percentage of total sugar in tetraploid tomatoes. Noguti, Oka and Ôtuka (1940) in a study of diploid and tetraploid *Nicotiana* showed that tetraploids contained smaller percentages of total sugar. Peto and Boyes (1940) claimed that triploid sugar beets contained 14.9 per cent more sugar than did diploid beets. Armstrong (1942) found no increase in percentage of sugar in triploid and tetraploid sugar beets when compared with diploids. The results of Sullivan (1944) indicated that tetraploid clones of rye grass grown in field rows contained more total sugar than the diploid clones. A comparison of tetraploid and octoploid *Trifolium repens*, grown in the field, showed no difference in nitrogen-free extract (total carbohydrate). The seeds of diploid and tetraploid barley were analyzed by Shao-Lin Chen and Tang (1945)

for nitrogen-free compounds. The diploid seeds contained 83.5 per cent nitrogen-free compounds while the tetraploids contained 80.2 per cent nitrogen-free compounds.

5. *Non-reducing sugars*.—Sullivan and Myers (1939) reported that the tetraploid plants of *Lolium perenne* L. contained a higher concentration of sucrose than the diploids. The results of Sullivan (1944) indicated that tetraploid clones of rye grass grown in field rows contained more sucrose than the diploid clones.

6. *Reducing sugars*.—Kostoff and Axamitnaja (1935) found that the amphidiploids of F<sub>1</sub> hybrids of *Nicotiana* had a higher content of reducing sugar. But according to these authors (1935a) there is little difference in the reducing sugar content of diploid and tetraploid *Petunia*. With diploid and tetraploid tomatoes, on the other hand, reducing sugars were higher in the tetraploids. Sullivan and Myers (1939) found more reducing sugar in tetraploid plants of *Lolium perenne* L. than in diploids. Noguti, Oka and Ôtuka (1940) showed that the tetraploid plants of *Nicotiana* contained less reducing sugar than the diploid plants. Barr and Newcomer (1943) reported that tetraploid cabbage contained a higher concentration of reducing sugar than did the diploid plants.

7. *Resin*.—Noguti, Oka and Ôtuka (1940) found a higher resin content in tetraploid *Nicotiana* plants.

8. *Fructosan*.—Sullivan (1940) could find no significant difference in the fructosan content of field grown diploid and tetraploid clones of rye grass.

9. *Lignin*.—Sullivan (1940) found no significant difference in the lignin content of field grown clones of diploid and tetraploid rye grass.

10. *Fiber*.—Sullivan and Myers (1939) could find no difference in crude fiber between clones of diploid and tetraploid rye grass. Sullivan (1940) reported that octoploid plants of field grown *Trifolium repens* had a lower fiber content than tetraploid plants.

11. *Discussion*.—Most investigators found that polyploid plants contain a greater percentage of total sugar, non-reducing sugar, reducing sugar and starch than do diploid plants. Diploid plants contain greater percentages of the structural constituents, cellulose, hemicellulose and crude fiber. The lessened amount of structural constituents in the tetraploids may be related to the decreased number of cells per plant in the tetraploid tissue. The increase in the percentage of soluble carbohydrates in polyploid tissue may be related to their higher water content.

A summary of the published data concerning the carbohydrate components in diploid and tetraploid plants is presented in Table 3.

### c. Other components

1. *Polyphenols*.—Kostoff and Axamitnaja (1935) were unable to find any difference between the polyphenol content of *Nicotiana* F<sub>1</sub> hybrids and their amphidiploids.

TABLE 3. Summary of the published data concerning the percentages of carbohydrate components in diploid and tetraploid plants. x signifies an increase; — signifies no difference.

	Starch	Cellulose	Hemicellulose	Total sugars	Non-reducing sugars	Reducing sugars	Resin	Fructosan	Lignin	Crude fiber
Dip. Poly.	Dip. Poly.	Dip. Poly.	Dip. Poly.	Dip. Poly.	Dip. Poly.	Dip. Poly.	Dip. Poly.	Dip. Poly.	Dip. Poly.	Dip. Poly.
Fern	x	x	x			x				
<i>Nicotiana</i>	x	x	x	x	x	x				
<i>Petunia</i>	—	—	—			—				
Tomato	x	—	x	x	x	x	x	x	x	x
Rye grass					x	x	x	x	x	x
Rye grass					x	x	x	x	x	x
Sugar beet					x	x	x	x	x	x
Cabbage	x									
Clover				—					x	
Barley				x						

2. *Nicotine*.—Kostoff and Axamitnaja (1935) found that the amphidiploids of  $F_1$  *Nicotiana* hybrids contained a higher percentage of nicotine. The nicotine content of a tetraploid *Nicotiana* was found to be higher than that of a diploid strain by Noguti, Okuma, and Oka (1940). Noguti, Oka, and Ôtuka (1940) confirmed the higher nicotine content of the tetraploid *Nicotiana*.

3. *Organic acids*.—Kostoff and Axamitnaja (1935) found no consistent difference in the percentage of citric acid in *Nicotiana*  $F_1$  hybrids and their amphidiploids. Kostoff (1938) investigated the citric acid content in allopolyplloid hybrids of *Nicotiana*. He found no consistent difference between the hybrids and their 5th generation of amphidiploids. The amphidiploids gave both higher and lower results than either of the parents. Noguti, Oka, and Ôtuka (1940) found a greater percentage of organic acid in the tetraploids of *N. rustica* and *N. Tabacum* var. Yellow Orinoco.

4. *Crude fat or other extract*.—Noguti, Oka and Ôtuka (1940) found that the tetraploid of *N. Tabacum* var. Yellow Orinoco had a higher ether extract than the diploid. The results of Shao-Lin Chen and Tang (1945) showed the seeds of tetraploid barley to contain 2.6 per cent ether extract while the diploid seeds contained 2.2 per cent ether extract.

5. *Discussion*.—It is evident from the published data that the amount of many constituents of the plant body may be altered by an increase in the number of chromosomes.

#### d. Vitamins

1. *Vitamin C*.—The early development of convenient methods of assaying ascorbic acid in plant tissue has resulted in a mass of experimental work. The relative ease with which vitamin C can be determined by the guinea pig biological assay, or by the colorimetric indophenol titration method has stimulated many workers to study the effect of various factors on the vitamin C content of plant tissues.

In 1931, Crane and Zilva suggested that there might be a connection between vitamin C content and the number of chromosomes in apples. In 1932, these authors reported a higher vitamin C potency in triploid as compared to diploid apples. Sansome and Zilva (1933) produced tetraploid tomatoes by the decapitation-callus method and investigated the indophenol-(dimethylamino-phenylindophenol) reducing capacity of the tetraploid and diploid tomato fruits. The tetraploid material had an indophenol-reducing capacity about twice that of the diploids. This result was verified by a biological assay with the guinea pig. The authors used tomatoes of different genetic constitutions and concluded that the vitamin C activity was independent of the genetic character of varieties tested. Key (1933) could find no difference in the vitamin C content of diploid and tetraploid tomatoes of the same genetic constitution. McHenry and Graham (1935) found a higher vitamin C content in tetraploid tomatoes

than in diploids. Göthlin (1935), using the guinea pig method of assay, reported that eight diploid apple varieties averaged 5.35 mgm. of ascorbic acid per gram, while 4 tetraploid varieties averaged 12.00 mgm. Sansome and Zilva (1936) confirmed their earlier data which indicated that tetraploid tomatoes contained a higher vitamin C content. Oka (1942) induced polyploidy in several varieties of tomato (Burbank, Ponderosa, Acte, Cooper's Globe, and Red Cherry) and concluded that the tetraploids contained more vitamin C than did the diploids. Darlington (1942) listed the vitamin C content of a number of rose fruits, and showed that the ascorbic acid content became higher as the chromosome number was increased; 2N plants contained 0.08 per cent while 8N contained 1.20 per cent. Barr and Newcomer (1941, 1942) determined vitamin C photometrically in diploid and tetraploid cabbage and discovered that the tetraploid plants contained more ascorbic acid than did the diploid—2N contained 48.40 and the 4N contained 59.95 mgm. per 100 gm. fresh tissue. Their later data showed that the 2N plants contained 53.51 mgm. and the 4N contained 63.46 mgm.

2. *Riboflavin*.—Smith and Olmo (1944) analyzed the fresh juice of diploid and tetraploid grapes for riboflavin using the microbiological assay method (*Lactobacillus casei e*). They could find no significant difference in vitamin content between the diploids and tetraploids.

3. *Pantothenic acid*.—The concentrations of pantothenic acid in the fresh juice of diploid and tetraploid grapes was shown by Smith and Olmo (1944) to be about the same.

4. *Carotenoids*.—Randolph and Hand (1940) carried out a rather extensive survey of the carotenoid pigments, beta-carotene and cryptoxanthin, precursors of vitamin A, and of zeaxanthin which has no relationship to vitamin activity, in commercial samples of hybrid corn and in some other diploid and tetraploid strains. A comparison was made of cell-volume relationships and of the carotenoid content of pure yellow diploid corn carrying the three dominant genes, YYY, for yellow and a derived tetraploid carrying the doubled number of genes. Analyses were made of the mature endosperm cells. There was a 40 per cent increase in the total carotenoids in the tetraploid material. A microscopic examination of the endosperm cells showed that the tetraploid cells were much larger than the diploid cells, the ratio of their volumes being 3.6:1. The data of these authors may be summarized as follows:

Proportional differences between the endosperm of diploid and tetraploid strains of yellow corn

Item	Diploid	Tetraploid
Cell volume	1	3.6
Carotenoid per unit volume	1	1.4
Genes per cell	1	2
Genes per unit volume	1	0.55
Carotenoid per cell	1	5
Carotenoid per gene	1	2.5

Straub (1940) investigated the carotenoid content of the "yellow spot" on the lower lip of *Torenia Fournieri*. The relative carotenoid content per cell of the polyploid series ran as follows: 2N—1, 3N—1.8, 4N—3.5, 6N—5.3, and 8N—6.1. Freisleben (1942) in a study of tetraploid barley could find no difference in carotene content of diploids and tetraploids. Sullivan (1944) found the carotene content of octoploid white clover to be lower than that of tetraploid plants.

5. *Discussion.*—Most of the published data indicate that polyploidy is associated with an increased ascorbic acid content of plants. How much of this increase might be due to differences in rates of growth, or in the moisture content, can not be determined since many of the investigators do not report the necessary data. Randolph and Hand (1940) discussed their findings in relation to the increase of the carotenoids of tetraploid corn and suggested "that there are two categories of gene action in the autotetraploids: (1) cumulative gene action, which yields percentage increases and accounts for the distinctive traits of autotetraploids other than those that may be attributed directly to the presence of an increased number of chromosome sets, and (2) non-cumulative gene action, which yields percentage decreases when the percentages of other constituents are increased." Smith and Olmo (1940) suggested several possibilities as to why chromosome doubling did not increase the riboflavin and pantothenic acid content of grapes. In the first case, if it is assumed that vitamin production is controlled by gene action, then the fact that doubling the number of genes did not increase vitamin production might indicate that a certain maximum threshold of production had already been reached in the diploid. The second explanation might be based on the supposition that a certain balance exists in vitamin production; the doubling of the genes which control synthesis is counterbalanced by the doubling of other genes utilizing or destroying the vitamins at equal rates.

#### e. Pigments

1. *Anthocyanin.*—Straub (1940) determined the red anthocyanin pigment from the petals of diploid and tetraploid *Impatiens Sultani*. The tetraploid flowers contained more pigment than the diploids.

2. *Chlorophyll.*—Pirschle (1941a) investigated the chlorophyll content of autopolyplid plants. On the fresh weight basis, the leaves of all tetraploids contained less chlorophyll than those of the diploids. However, per unit of area, the tetraploids were richer in chlorophyll: 110–120 per cent for *Antirrhinum* and *Epilobium* and 150 per cent for *Torenia*, while there was no change for *Impatiens*. The reason for these observed differences was the greater thickness of the tetraploid leaves. Freisleben (1942) found no differences in chlorophyll and xanthophyll in diploid and tetraploid barley. Györffy (1941) investigated the pigment content of different autotetraploid plants, *Antirrhinum majus*, *Epilobium*, *Lycopersicum*, etc., and found

that the pigment content of most of the tetraploids of the different species was higher than that of the diploids.

#### f. Enzymes

In connection with their physiological studies on the seeds and plants of diploid and tetraploid barley, Shao-Lin Chen and Tang (1945) investigated the enzyme activities. They studied catalase activity by measuring the O<sub>2</sub> evolution from finely ground powder of barley seeds in a Warburg microrespirometer. The tetraploid barley yielded 58 cmm. of oxygen while the diploid barley evolved 23 cmm. of oxygen. They found that the relative diastatic activity of tetraploid malt extract was 20, and that of the diploid malt extract was 11. They also studied the dehydrogenase activity of leaf extracts of diploid and tetraploid barley. Their work indicated that the diploid and tetraploid plants had similar dehydrogenase systems. The leaf extracts of both diploid and tetraploid plants were without effect in reducing methylene blue in the presence of succinic acid, *e*-malic acid, lactic acid, citric acid, and Ca-glycerophosphate. Both diploid and tetraploid leaf extracts effected a reduction of methylene blue in the presence of ethyl alcohol, glycine, dl-alanine, glutamic acid, cystene, and l-cystine. The rate of reduction was faster in the presence of the leaf extract from diploid barley.

#### g. Discussion

The organic components in polyploid plants have been more extensively studied than the other components. This is probably the result of their greater economic importance for human and animal nutrition. Randolph (1941) points out, "If such important constituents such as the protein content of cereals, the vitamin content of fruits and leafy vegetables and the sugar content of sugar-producing plants are increased significantly by chromosome doubling without attendant deleterious effects, induced polyploidy will most certainly become an increasingly important method of plant breeding."

When percentage increases of certain constituents are found, there must be a corresponding decrease in other constituents. It is impossible to determine such relative changes from published data because many workers have studied only single constituents. A number of investigations show a decrease in total nitrogen in the tetraploids accompanied by an increase in carbohydrate fractions such as total sugars.

The enzyme studies associated with polyploidy are of considerable interest because they indicate inherent differences in diploid and tetraploid cells. Additional studies in known plant enzyme systems might give further insight into fundamental physiological differences between diploid and polyploid cells. The enzyme studies are also of interest because of the role

that certain vitamins play in making up enzymes. Differences in the vitamin content of diploid and polyploid plants might be correlated with different enzyme activities.

## 2. INORGANIC COMPONENTS

### a. Total ash

The published data concerning the total ash or the mineral components of diploid and related polyploid plants are scarce. Kostoff and Axamitnaja (1935) determined the total ash of  $F_1$  hybrids and their amphidiploids of *Nicotiana*. In the  $F_1$  hybrid (*N. rustica*  $\times$  *N. paniculata*), the ash content was 12.61 per cent; the amphidiploid has an ash content of 23.20 per cent. The  $F_1$  hybrid (*N. glauca*  $\times$  *N. Langsdorffii*) had an ash content of 16.97 per cent while the amphidiploid contained 17.72 per cent. Kostoff and Axamitnaja (1935a) investigated the chemical differences between diploid and tetraploid tomatoes (var. *Micado*) and *Petunia*. The diploid tomatoes contained 24.80 per cent ash, the tetraploids 21.10 per cent, while the *Petunia* diploids contained 20.60 per cent ash and the tetraploids 22.50 per cent. Schlösse (1937) determined the ash in several diploid and polyploid forms of tomato. Diploid *Lycopersicon cerasiforme* plants contained 684 mgm. of ash per plant, while tetraploid plants contained 797 mgm. per plant. *L. racemigerum* diploids had 519 mgm. per plant and tetraploids had 577 mgm. of ash per plant.

These data recalculated as ash per gram of dry matter showed that *L. cerasiforme* diploids contained 179 mgm. of ash and tetraploids 166 mgm., and *L. racemigerum* diploids contained 137 mgm. and the tetraploids 139 mgm. of ash. Gries (1940) found the ash of diploid barley to be 11.3 per cent of the dry weight and the tetraploid barley to contain 16.4 per cent ash. Noguti, Oka, and Ôtuka (1940) analyzed *Nicotiana* diploids and polyploids for soluble ash. They divided their leaf material into upper and lower, depending on position occupied on the stem, and into medium and good quality. The soluble ash content of the tetraploids was in all cases higher than that of the diploid material. Pirschle (1941) found the ash content of tetraploid *Petunia* to be slightly higher than that of diploids during the early stages of growth, but as the plants approached maturity, the ash content of the tetraploids became considerably greater. Barr and Newcomer (1943) reported that the ash content of normal diploid cabbage was 4.94 per cent of the dry weight, while the tetraploid cabbage contained 3.99 per cent. Sullivan (1944) found the ash content of field grown tetraploid *Trifolium repens* to be 13.85 per cent of the dry weight, while the octoploid form contained 14.07 per cent ash. Shao-Lin Chen and Tang (1945) showed that the tetraploid seeds of barley contained 2.5 per cent ash while the diploid seeds contained 1.6 per cent ash.

### b. Metallic elements

Noguti, Oka and Ôtuka (1940) analyzed the mineral constituents of field grown, flue-cured tobacco (*N. Tabacum* var. Yellow Orinoco). The tetraploids were found to contain more CaO, K<sub>2</sub>O, and MgO. Pirschle (1941) determined K, Ca, Mg, P, Fe, and Mn in diploid and tetraploid *Petunia*. The tetraploids contained slightly more K and Mg than the diploids. Rohweder (1937) studied the chromosome number of *Dianthus* plants found in a region with highly calcareous soils. Diploids did not grow well on the calcareous soil, but if the chromosome set was doubled the plants thrived. There were many other tetraploid plants growing in this calcareous region.

### c. Acidic elements

Noguti, Oka, and Ôtuka (1940) found that tetraploid tobacco (*N. Tabacum* var. Yellow Orinoco) had less SO<sub>3</sub> and P<sub>2</sub>O<sub>5</sub> than the diploid plants.

### d. Discussion

There have been no extensive studies on the mineral composition of diploid and polyploid plants. The one paper by Noguti, Oka, and Ôtuka

TABLE 4. *Summary of the published data concerning the inorganic components in diploid and polyploid plants.*

	Total ash		Soluble ash		
	Diploid	Polyploid	Diploid	Polyploid	
<i>Nicotiana</i>		x			
<i>Nicotiana</i>				x	
Tomato	x				
Tomato	x				
Tomato	-----				
Barley		x			
<i>Petunia</i> , early growth	x				
<i>Petunia</i> , maturity		x			
Cabbage	x				
Clover		x			
Barley		x			
<i>Individual ash constituents</i>					
	SO <sub>3</sub> Dip. Poly.	P <sub>2</sub> O <sub>5</sub> Dip. Poly.	CaO Dip. Poly.	K <sub>2</sub> O Dip. Poly.	MgO Dip. Poly.
<i>Nicotiana</i>	x	x	x	x	x
<i>Petunia</i>				x	x

showed that the tetraploid plants contained greater percentages of the metallic elements and decreased percentages of the acid elements. Rohweder suggests the interesting possibility that chromosome doubling may increase the ability of a plant to utilize certain soil constituents. This particular problem may be of economic interest where soils are deficient or contain relatively unavailable forms of mineral nutrients.

The published data concerning the inorganic components of diploid and tetraploid plants are summarized in Table 4.

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## A Revision of Dyera (Apocynaceae)<sup>1</sup>

JOSEPH MONACHINO

(New York Botanical Garden, New York)

*Conspectus.*—In this paper a detailed bibliographical revision of Dyera is presented. All data available to the author which might bear taxonomic significance for the genus or its species are elaborated, and all the important non-taxonomic references are at least cited in the bibliography. This treatise is chiefly a compilation and lacks taxonomic finality. It does not even represent an outstanding advance in our taxonomic understanding of Dyera, though particular attention has been paid to any information which may serve for this purpose.

The major portion of the present study was conducted at a time when the herbarium specimens of the genus available in the United States were woefully inadequate. Recently, however, with the termination of the War, the material from Kew has been received for examination, thereby enabling me to formulate an opinion regarding the taxonomy of the group. Unfortunately I have been unable definitely to resolve one of the gravest problems concerning the genus, the true position of *Dyera Lowii* and *Alstonia polyphylla* in respect to each other and their specific separation from *D. costulata*. I have not seen the types of *Alstonia polyphylla*, *A. eximia*, and *A. grandifolia*, species which probably belong to Dyera.

By way of introduction, the following topics pertaining to Dyera are discussed: literature, uses, cultivation, produce, local names, abbreviation of herbaria and acknowledgments. In the taxonomic portion of the paper, the following order is adopted: generic description, citation of type species, references to illustrations, field observations, distribution. After a discussion, in which Dyera is accepted as being morphologically closest related to Alstonia and consisting of merely two not clearly defined species, follows a systematic treatment of all the names involved. A bibliography of 133 entries is appended.

*Literature.*—The Botanical Identity of Jelutong<sup>2</sup> by C. F. Symington, Botanist of the Forest Research Institute, Kepong, is an excellent taxonomic account of *Dyera costulata*, although not monographic in character. I do not find it possible at the present time to supplement or qualify his botanical treatment of *D. costulata*, for Mr. Symington had not only the opportunity to study the herbarium material at Kew, Singapore and Kepong, but also the benefit of considerable field observation in the Malay Peninsula, where Jelutong is well known both in the forest and in commerce.

<sup>1</sup> This contribution is made possible by the financial support of the Chicle Development Company.

<sup>2</sup> Jelutong has gained sufficient importance to be mentioned in Webster's New International Dictionary of the English Language, 2nd Ed. Vol. 2, 1942.

In this article, Symington reviews the history of *Dyera* with particular attention to the proposed differences between *D. costulata* and *D. laxiflora*. He concludes that the two are synonymous. As additional synonymy of *D. costulata* he lists questionably Miquel's *Alstonia eximia* and *A. grandifolia*, species which, however, were known to him only from description. *A. polyphylla*, it is suggested with reference to the authority of Heyne, may be *Dyera Lowii*. The ample description and detailed plate of *D. costulata* which follow are among the best available.

Citations of the specimens examined are omitted in Symington's treatment; no detailed distribution of *Dyera* is presented; and, although the author apparently accepts *D. Lowii* as distinct from *D. costulata*, he does not indicate the differences between these two species.

Similarly, references to the botanical distinction between *D. Lowii* and *D. costulata* by other authors are practically missing. M. E. G. Brown (in manuscript) presents several field differences in habitat, average dimensions, and presence of pneumatophores, characters which are useless in herbarium studies. E. M. Drees refers merely to the different altitudes above sea level in which the two species are found. H. N. Ridley (98, p. 95) notes minor dissimilarities in leaf-shapes, which he himself doubts (99) as being of specific value.

Good descriptions of *Dyera* and valuable distribution data are presented by King & Gamble, Burkill (16) and Ridley (97, 98). The field description and general information in Foxworthy's Commercial Timber Trees of the Malay Peninsula are particularly noteworthy. Judging by the frequency with which it is cited in the literature concerning *Dyera*, Burn-Murdoch's Trees and Timbers of the Malay Peninsula (not seen by me) probably deserves mention here.

Among the less important taxonomic contributions to the genus the following should be mentioned: Corson, Watson (127), Heyne, and Smith. Van Romburgh's notes on his various encounters with *D. Lowii* in Borneo, and particularly his field observations on the pneumatophores of this species are of interest. The original diagnoses presented by Miquel, Hooker (67, 68), and Baillon (4) are historically important.

Detailed reports of the occurrences of *D. Lowii* and *D. costulata* in Palembang and Lampoeng, Sumatra, appear in M. E. G. Brown's manuscript on the forest survey of these regions. This author's Forest Survey for Jelutong in Lingga and Singkep should also be included here.

Edwards & Mead's growth records of *Dyera* in sample plots, and Holtum's notes on the leaf-change periodicity and formation of fruits in *D. costulata*, are valuable original observations. Raciborski treats the vegetative morphology of the species.

Besides casual remarks on the timber of *Dyera* in various publications and a figure of the wood anatomy of *D. Lowii* in Foxworthy (45), the only signifi-

cant contributions to the study of the wood structure of this genus are those of Cockrell and Bargagli-Petrucci.

The literature on the silviculture, tapping, coagulation of the latex, and the commercial aspects of *Dyera* is extensive. The numerous contributions of Georgi in the Malayan Forester and the Malayan Agricultural Journal, extending from the year 1927 to 1935, and those of Eaton, Georgi & Teik in 1926 & 1927, and Watson & Georgi (Mss.) in 1945 are the most important ones. Greenstreet (1925), Corson (1927), Watson (127) (1935), Brown (1939 & 1940), and Smith (1940) are equally important. The following references are also significant: Burkill (16), Drees, Eaton & Dennett, Foxworthy (47), Heyne, Laan & Meurs, Ridley (98), Schidrowitz, Walton. Statistics on the exports and imports of Jelutong, and other data mostly borrowed from Heyne, appear in Vander Laan's Production of Gutta-Percha, Balata, Chicle and Allied Gums.

Numerous references to chemical studies in *Dyera* are found in Wehmer's *Pflanzenstoffe*. The outstanding ones cited in the Bibliography at the end of the present paper are those of Ellis & Wells, and Hillen on the resin extracted from Jelutong. Chute and Dubosc also experimented with this product. Pearson (89) quotes Ellis' essay on the use of Pontianak resin in the waterproofing of concrete. Cohen and Nöjd treat the Lupeol derived from *Dyera*, while Sack & Tollens and Alexander write about other compounds. Hinrichsen & Marcusson and Tilden are minor contributors.

The list of references presented in the Bibliography at the end of this paper does not include all those published on *Dyera*. However, it is hoped that the important contributions have been recorded and that the catalogue might eventually serve as a basis for a complete revision both bibliographically and taxonomically.

*Uses.*—The principal use of *Dyera* is found in its latex which has been used extensively as a basic material in the manufacture of chewing gum. It is estimated (unpublished survey, May 31, 1944) that the yearly average amount of Jelutong from 1912 to 1922 produced for this purpose was 30,500,-000 lbs.<sup>3</sup> According to Vander Laan (122, p. 65; source: Commerce and Navigation of the United States) the total imports in pounds of Jelutong into the United States for the years 1901 to 1925 have been as follows: 1901—9,371,087; 1902—16,850,821; 1903—13,984,817; 1904—14,887,416; 1905—19,104,911; 1906—21,390,116; 1907—28,437,660; 1908—22,803,303; 1909—24,826,296; 1910—52,392,444; 1911—51,420,872; 1912—48,795,268; 1913—45,345,338; 1914—24,926,571; 1915—14,851,264; 1916—27,858,335; 1917—23,376,389; 1918—21,399,377; 1919—18,662,702; 1920—12,705,923; 1921—3,908,401; 1922—5,229,505; 1923—10,226,281; 1924—13,809,583; 1925—15,118,547. Thus, the yearly amount for the period has always exceeded 3

<sup>3</sup> J. G. Watson in Burkill (16, p. 877) writes: "Between 1913 and 1922 its [Jelutong's] exploitation would have ceased everywhere, except that it was used on a small scale."

million pounds and in 1910 exceeded 52 million. Howes estimated in 1930 that the American markets were capable of absorbing about 5000 tons of Jelutong annually. The United States is the largest consumer of Jelutong. See Vander Laan (122, pp. 63, 64, 65) for further statistics.

With the intensive exploitation of Jelutong which will now probably be resumed as a peacetime activity, what is the outlook for the future supply of the gum? While the habit of chewing gum is apparently steadily increasing, it was reported in the 1944 survey that the Jelutong area about Pontianak in Dutch Borneo was exhausted. The suggestion is made that this lack might be replaced by a possible substantial production in East Borneo. The blame for exhaustion of Dyera in some areas is attributed to the method of working the trees. Watson (127, p. 59) writes: "Where such operations [silvicultural treatment applied under scheme felling] have been carried out in areas containing *Jelutong* the percentage of this species has increased to an extent that justifies the assumption that there need be no fear of a shortage in the future, and that this tree will not only continue to yield an abundance of latex but will, in due course, provide a surplus of timber suitable for export." He continues (p. 60): "Experience in areas treated under scheme felling has shown that *Jelutong* recovers very rapidly from felling damage and that it coppices readily. Examination of natural regeneration invariably discloses a high percentage of saplings that have originated as stool shoots."

The market demands for Jelutong are now controlled almost exclusively by the chewing gum industry. Watson does not believe that the uses of Jelutong can be widely extended. To a very limited extent, principally in the earlier period, other uses for the latex of Dyera have been reported. Pontianak found some employment in the manufacture of inferior or secondary rubber goods for which elasticity was not a prime consideration; in the adulteration of the better rubbers or gutta percha for production of the cheaper qualities of rubber articles, or in compounds and fillings or as a binding ingredient in mixings. Dyera product is reported to have been utilized in making architectural work water-tight, as in waterproofing mixtures applied to the walls, floors and roofs of houses; to make mouldings of picture-frames; in various assorted articles or goods, as rubber shoes, asbestos, celluloid and linoleum.

Clercq notes doubtfully that the latex of *D. costulata* is drinkable when hot and states that it tastes somewhat like milk. Corson remarks that the coagulated rubber is pleasant to the taste. Hasselt & Boerlage (57, p. B15) refer to the latex as tasting like milk, and add that it is a good means against blisters on the tongue.

The caoutchouc from Dyera comprises only about 20 per cent of the total dry weight of the coagulum, the remainder being chiefly resin. Chute (20, p. 351) reports: "Pontianak resin has been used with some success, as one producer claims to have sold 400 tons to a single varnish company, and car-

loads to several others, and the companies who have used it assert that after a year's test they find the varnishes with the resin in them in better condition than those without."

The resistance of Pontianak resin to the action of aqueous alkali solutions has led to its application as a coating material for cement and concrete, or for waterproofing concrete (Ellis' patent No. 999,493). The resin has also been used in paints or as priming for concrete (Ellis' patent No. 999,708) and for sizing paper (Ellis' patent No. 1,007,681). The volatile oils resulting from the destructive distillation of the rubber resins have been suggested as a raw material for preparing isoprene.

The wood of Dyera is very soft, light, even-grained and very easily worked. It is not durable, for when in contact with the ground it is usually destroyed by termites in less than six months, and it is subject to the attacks of boring beetles. The timber of Dyera is not suitable for structural purposes because of this weakness and lack of durability. However, Ridley (94, p. 250) suggests that it might be employed for walls and partitions of houses. The wood was formerly used locally for manufacturing Chinese clogs (the Malay "trompah" or wooden sandals in Singapore), and is said to be excellent for making patterns. It has also been reported serviceable for furniture, chests, match sticks, match boxes, packing cases, and drawing boards. Low reports that Jelutong wood was used by undertakers ("cheaper grade of Chinese coffins," Foxworthy, Indo-Malayan Woods). Hasselt & Boerlage (57, p. B20) record that a gambier is baked from the wood.

Amongst the aborigines of the Malay Peninsula, the Mintira and Berembun (Skeat & Blagden) and the Benua (Burkill, 16, p. 876) have been reported to contrive caps for their quivers from small blocks of Jelutong wood. The Benua have been observed to also use the wood to make mouthpieces for their blowpipes.

Winkler states that the roots of Dyera served as substitutes for cork and for making ax handles. Corson (26, p. 48) reports how the follicles, which burn with a steady bright flame, are sometimes used by the natives of Sarawak as torches, or are kept merely glowing to keep mosquitoes at bay by the pungent smoke they emit. Hasselt & Boerlage (57, p. B15) also had referred to their use as torches (in remarks under *Alstonia grandifolia*), and added that the fruits of *D. costulata* are burnt as a resin and used as ointment against sores.

*Cultivation.*—Dyera is widely distributed in the Malay Peninsula, Sumatra and Borneo. It is classed by Foxworthy (47, p. 109) as nineteenth in order of abundance of the commercial trees of the Malay Peninsula. This author, however, doubts whether there is in the Peninsula as a whole an average of more than one matured tree to nine acres. The difficulty always attending the exploitation of a product in the wild, coupled with Dyera's encouraging habit of fast growth after an initial establishment period, its

adaptability and great recuperative power, have suggested the cultivation of this valuable giant tree, but without conclusive results. Brown (12, p. 14) reported in 1939 that the British and Dutch Department had endeavoured to form artificial plantations with *D. costulata* without very great success. On the other hand, Smith (114, p. 317) announced in 1940 that a seven year old plantation in Sarawak was reported to be making good progress. Watson (127, p. 58) wrote in 1934: "Sporadic attempts have been made from time to time to start plantations on lines similar to those adopted for the cultivation of Para rubber. Most of these schemes failed to materialize owing to the difficulty of obtaining supplies of seed. Collection of seeds is extremely difficult. Gathering the fruits is, more often than not, a practical impossibility owing to their distance from the main branches and the difficulty of climbing the long clear bole that is so characteristic of the tree. And even if the fruits are secured they are useless unless they are just ready to open, a condition that is by no means obvious at close quarters, much less from the ground level. Attempts to encourage collections by the offer of substantial rewards have been singularly unsuccessful." In the following year, in Burkhill's Dictionary (16, pp. 881-882), Watson wrote: "From the behaviour of the tree in open places in the forest, from such meager growth statistics as are available, and from our limited nursery experience, the indications are that the tree could be grown under plantation conditions and might be expected to reach tappable size (as judged by Para rubber standards) in about 15 years." The difficulty, he insists, is in obtaining ripe seeds: "The fall of these featherweight seeds is so gradual that they are scattered over a very extensive area. That few of them reach the seedling stage is evident from the sporadic occurrence of the tree and the difficulty that has been experienced in obtaining, even at exorbitant prices, sufficiently naturally sown transplants to stock a 10-acre experimental plot." To facilitate the collection of the seeds, Corson (26, p. 51) suggests gathering the fruits before they are fully ripe, to slit and suspend them in sheds to ripen and dispel their seeds artificially.

The seeds of Dyera are said to be difficult to handle in artificial planting but to germinate readily, requiring 11-15 days (35-50 days, according to Derry) or as little as 10 and as long as 90 days. Watson (127, p. 58) writes that the growth is not very rapid in the early stages, six month old seedlings being only about 3 inches high, and that it is of very uneven rate in spite of identical treatment. Individual heights of as much as 12 feet have been recorded at 3 years of age (19 feet at 4 years), but the average of a batch of transplants set out under favourable conditions was little more than 3 feet. "It seems, therefore, that like many other of our indigenous trees, Jelutong requires a protracted establishment period, and that it does not embark on rapid growth until its root system is well developed."

Young saplings of Jelutong are very susceptible to injury but have great

powers of recuperation, and once established *Dyera* is said to be one of the most rapidly growing trees in the Malay Peninsula. Specimens under observation have attained a girth of 18 inches at the end of 5 years. "The highest recorded girth increment for a single tree is 4.2 inches over a period of 4 years (maximum 5.0 inches in 1927), which is a record for measured trees of any local species," Watson (127, p. 59) states. "On the basis of a considerable number of annual measurements of dominant trees in sample plots it has been estimated by Edwards in Malayan Forest Record No. 9 that Jelutong takes about 46 years to reach a girth of 5 feet and 70 years to reach 7 feet, exclusive of the time required for establishment, which, according to plantation experience, should be about 4 years."

*Produce.*—According to Watson, high-yielding trees 7 ft. or more in girth will give about 20 oz. of latex a day, or about 400 oz. a month coagulating to 8 lbs. of commercial Jelutong. One tree might yield 67 lbs. per year. Pearson (88) calculates it is capable of yielding 100 lbs. of gum when cut down. Corson estimates a single laborer can tap between 25 and 30 trees a day and collect from 3 to 4 or more gallons of latex. A tree tapped once in 3 days, he states (26, p. 52), has been found satisfactory.

*Local names.*—The best known of the popular names of *Dyera* is *Jelutong*. Easily recognizable variant spellings of *Jelutong* are found in literature: *Dgiuluton*, *Dgiulutong*, *Djelutang*, *Djeloetoeng*, *Djelutung*, *Edjelotong*, *Gelutong*, *Jeluntong*, *Telutong*. The name is applied interchangeably to the tree or its gum. The rubber is usually called *Gutta Jelutong* (*Ghettà Dgiulutong*, or with the components of the name appearing as linguistic or orthographic variants, e.g. *Gētah*). Sometimes reference is made to the timber of *Jelutong*, the habitat or some particular descriptive feature: *Kayù* (wood) *Jelutong*, *Hill Jelutong* (*Dyera costulata*, the swamp *Jelutong* being *D. Lowii*), *Jelutong Daun Lebar* (broad-leaved), *Jelutong Daun Merah* (red-leaved), *Jelutong Pipit* (Sparrow's *Jelutong*).

*Jelutong* is a characteristic tree rarely mistaken for any other. When this name designates the gum rather than the tree, however, it frequently stands for a mixture derived from *Dyera* and other genera. Ridley (100, p. 50) writes in reference to *Getah Jelutong* or *Pontianac*: "it is probable that the material as met with in commerce is a mixture of guttas derived from different sources. It has been stated, in fact, that it is the custom of the natives to mix the latex of the *Jelutong* tree with that derived from different species of *Willoughbeia*, which yield an inferior rubber." Vander Laan (122, p. 61) quotes a translation from Heyne's Wild Rubber: "*Dyera Lowii* Hook. f. yields *Jelutong*, as does *Dyera costulata* Hook. f. Other species which probably yield *Jelutong* are *Alstonia Scholaris* R. Br., *Alstonia grandiflora* Miq., *Alstonia eximia* Miq., and *Rauwolfia spectabilis* Boerl." Karling (72, pp. 77, 81) remarks that, according to Heyne and Corson, the names Dead Borneo, Pontianak, and Gutta *Jelutong* are applied to the above species of

Alstonia and Rauwolfia as well as to Dyera. It should be noted, however, that *Alstonia grandifolia* Miq. ("*A. grandiflora*" is an error for this) and *A. eximia* are probably merely synonyms for *Dyera costulata*. King & Gamble (p. 439) state that a Wray collection of *Alstonia angustiloba* Miq. from Perak was given the vernacular name Jelutong.

Ridley (94, p. 249) received a plant named Getah Jelutong from British North Borneo which obviously is neither Dyera nor Alstonia or Rauwolfia: "I have received another plant from British North Borneo at Labuk Bay under the name of Getah Jelutong from Mr. Wade. This, a branch with leaves only, has the leaves scattered, not in whorls; they are rather thin textured, very long and narrow lanceolate acuminate, 8 inches long, 2" wide, with a slender petiole an inch long. It is probably not a *Dyera* at all, but further material is required."

In Malay Plant Names, Ridley (93, p. 260) attributes the local name Jelutong Badak to *Tabernaemontana corymbosa* Roxb. and Jelutong Laut (Singapore) to *Euphorbia atoto* Forst. The identification by Murton (84) of *Alxyia* sp. for Gutta Jelutong was through error.

The following additional local names for Dyera or its gum appear in literature (the diphthong *æ* is equivalent to *u*; when names are identical except for this variant spelling only those with *æ* will be listed): *Badang*, *Badong* & *Bedok* (in Sakai), *Besk* or *Bresk*, *Bulantau* (south Borneo), *Dead Borneo*, *Fluvia* & *Gambria* (the gum; Pearson), *Gapeek* (west Sumatra; Cockrell), *Handjalotong* (south-east Borneo; under *Dyera Maingayi*; Clercq), *Laboeai* or *Laboei* or *Laboewai* or *Laboeweh* (Sumatra), *Lu Tong* (Siamese, Setul), *Malaboeai*, *Melaboeai* (Sumatra), *Medang Palai* or *Medang Pelai* (Malaya; under *Dyera Maingayi*; Clercq), *Mesenteh* (under *Alstonia polyphylla*; Heyne, 60, p. 64), *Njahtoeng*, *Palai* (Malaya; under *Dyera Maingayi*; Clercq), *Paloja* (a base produced by Jelutong mixed with other substances; Smith, p. 306), *Pantoeng*<sup>4</sup> or *Pantoeng Kapoer* or *Pantoeng Senaman* (Borneo), *Pelai* (south east Borneo under *Dyera Maingayi*; Clercq), *Plaai* (under *Alstonia eximia*; Kurz), *Poelai* (under *Alstonia polyphylla*; Heyne, 60, p. 64), *Pontianak*, *Pulih*,<sup>5</sup> *Susu*.<sup>6</sup>

<sup>4</sup> Boerlage (10, pp. 15 & 12), deriving his data from Van Romburgh, ascribes the name Pantoeng to *Alstonia scholaris* from Boentok and *Rauwolfia spectabilis* from Moeara Teweh, as well as to *Dyera Lowii* from Medara and Pangenang, Borneo.

<sup>5</sup> The name Gutta Pulih appears on the label for a *Dyera costulata* collected in the Garden Jungle, Singapore. The vernacular Pulai, however, is more commonly applied to *Alstonia* spp. There is available a collection distributed as *Rauwolfia samarensis* Merr. from British North Borneo, which is noted as having the local name Pulai. This plant is very closely related to, if not identical with, *Rauwolfia spectabilis* (Miq.) Boerl.

<sup>6</sup> A gum named Gutta Susu received from the Langkawi Islands was identified as from Dyera in the Bulletin of the Imperial Institute (2, p. 15). Watson (16, p. 876) and Ridley (93, p. 96) affirm that one of the alternative names for Dyera rubber is Getah Susu. However, this vernacular epithet is applied by Vander Laan (122, p. 68) to *Willughbeia firma*, a vine found commonly in the Netherlands East India islands. Heyne (59, p. 52, 60, p. 1272) notes Getah Soesoe (*æ* is pro-

*Abbreviation of herbaria and acknowledgments.*—The depositories of the specimens examined are abbreviated as follows: A—Arnold Arboretum, Jamaica Plain; C—University of California, Berkeley; G—Gray Herbarium, Cambridge; K—Royal Botanic Gardens, Kew; M—Missouri Botanical Garden, St. Louis; NY—New York Botanical Garden, New York; P—Museum d'Histoire Naturelle, Paris; US—United States National Herbarium, Washington; Y—Yale School of Forestry, New Haven. Acknowledgment is here made to the directors and curators of the institutions listed for their generous loans of herbarium material, and my particular gratitude is expressed for the aid rendered me by Mr. B. A. Krukoff and Miss Barbara Hoskins, Drs. H. A. Gleason and H. N. Moldenke.

DYERA Hook. f., Jour Lin. Soc. Bot. 19: 293. Aug., 1882.

Distinctive giant trees of rapid growth, copiously laticiferous, usually more or less conic in shape, commonly 50 m. in height and 65 cm. diam., occasionally reaching over 66 m. in height, 3 m. diam., and 36 m. to first branch, the trunk rounded, columnar, without buttresses (often with slight swelling at base), with or without pneumatophores, the crown with 33–50 m. spread; BARK 0.5–2.6 cm. thick, corky, smooth or warty or rough, often cracking into small irregularly shaped pieces, without longitudinal furrows, grey or greyish red to brown or almost black, with reddish color when cut, the inner bark thick, brittle, pale brownish or dull whitish, with abundant latex which also flows in small amounts from outer part of wood; BRANCHLETS verticillate, stout, rigid, sometimes swollen at termination of last season's growth, 5–8-angled with strong ridges in line below petioles, deeply channelled, often minutely rugulose, glabrous, brownish or reddish brown when young, dark or light grey when old; leaf-scars shield-shaped towards termination of branchlets, becoming crescent-shaped lower down, sometimes with orbicular gland-scar above, almost touching around branchlets, separated by ridges; gland at axil of petiole, prominent, rigid, deltoid-lanceolate, up to 4 (–7) mm. long and 3 (–4) mm. broad, sometimes deciduous together with petiole, as numerous as number of leaves in whorl and together forming an ungulate connivent (glands sometimes rather spreading) ring to protect terminal bud; LEAVES verticillate towards ends of branchlets, usually about

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nounced as *ou* in would) for this species of vine; and Boerlage (10, p. 5) also gives this name for *Willughbeia firma* from Soengai Boeian and Telok Kemorin, Borneo. Morris (83, pp. 44, 46, 47), too, regarded Gutta Susu as from *Willughbeia* (and also *Leuconotis*). Van Romburgh (108, pp. 23 & 24), while ascribing Djintaäns Soesoe to *Willughbeia firma*, notes that Getah Soesoe or Borneo Rubber is a product of many lianas. Beccari, under Nota Sopra i Produttori di Gomma Elastica in Sarawak, cites Ghettà Dgianta-an Susù as the product of *Willoughbeia firma* and *Urnularia oblongifolia*. In the Journal of the Royal Asiatic Society (93, p. 260), Ridley attributed the name Susu (Bunga) to *Tabernaemontana coronaria* Br. H. L. Gerth van Wijk, in A Dictionary of Plant Names, lists Gutta Susu for *Urceola elastica*.

7 (6–8) in a whorl (opposite in seedlings), deciduous with new leaves appearing shortly, glabrous; petioles 2–6 (–7) cm. long, drying blackish or brown; blades very variable in shape and size, elliptic, oblong to obovate or oblanceolate, up to 23 cm. long (–43 cm. in shoots) and 12 cm. broad, rounded or slightly subcordate to obtuse, or cuneate-attenuate at base, frequently asymmetrical, the apex short-acuminate to rounded or slightly retuse, the margins often faintly undulate, incurved, coriaceous to chartaceous, the midrib keeled on upperside, prominent on underside, the principal lateral or secondary nerves 13–30 pairs, with a distance of 4–18 mm. apart near middle of blade, minor intermediaries sometimes present, diverging mostly upwards from midrib, arcuate, joined by a marginal nerve, the reticulation prominent in matured leaves, the upper surface typically bright green, glossy, drying a reddish or yellowish brown, the lower surface pale bluish green, glaucous; INFLORESCENCES axillary at base of season's new growth (axil of penultimate whorl of leaves or their scars), rarely appearing terminal by suppression of new growth, in ample paniculate many-flowered cymes, up to about 18 cm. long, bracteolate, glabrous, the primary peduncle (2.5–) 6–9 (–12) cm. long, strongly angled, the infl. branches usually in 4–6-veticils along infl. rachis, the pedicels up to 10 mm. long, the bracteoles minutely triangular or linear, occasionally foliaceous at base of primary veticil, deciduous; CALYX-LOBES 5, quincuncial, ovate to ovate-orbicular, 0.6–1.3 mm. long and 1.2–1.5 mm. broad, rounded to subacute at apex, glabrous, not ciliate, flattened or faintly keeled, sometimes minutely jagged at edges, the glands at base within short, in one series, close together, about 4; CORILLA developing with new leaves, hypocrateriform, white, slightly fragrant; corolla-tube short, cylindric-urceolate, slightly widened upwards, hardly dilated at region of anthers, 1.2–3 mm. long, faintly angled in line with sinuses outside, glabrous except for a line of minute hairs within at level with or a little below insertion of filaments, this pubescence developing into denser tufts alternate with stamens; corolla-lobes oblongish to linear-oblong, much longer than corolla-tube, mostly 3–9 mm. long and 2–3.8 mm. broad, auriculate and asymmetric at base, obtuse at apex, glabrous, veiny, sinistrorse contorted in bud (viewed externally), not twisted, spreading at maturity; STAMENS inserted a little below middle of corolla-tube, the anthers on very short but distinct filaments, oblongish to lanceolate, shallow-cordate at base, 0.9–1.6 mm. long, their polleniferous cells below, the upper half of anther consisting merely of sterile connective produced into a thickened fleshy appendage, terminated by a short point which is sometimes inflexed, reaching up to throat of corolla-tube or a little exserted; OVARY apocarpous but appearing as single with two cells semi-orbicular, about half or more inferior, densely pubescent on upper part, rounded at apex, without glands or apparent disk, the ovules numerous, pluriseriate; STYLE very short, up to 0.16 mm. long, the thickened clavuncle annular-cylindric, 0.15–0.25 mm. long, glabrous, without membranous

fringe, the stigmatic-apiculi two, about 0.31–0.32 mm. long, blunt at apex, microscopically papillose: MERICARPS two large cylindric woody follicles, up to 40 cm. long and 4 cm. broad, connate at base on a thickened peduncle, dehiscing along a dorsal suture, diverging at maturity and finally curved backwards so as nearly to touch at apices; SEEDS numerous, 12–24 in each follicle, crowded in two rows, very thin and light, peltate, elliptic to oblong, markedly papillose on their surfaces, surrounded by an elliptic to oblong membranous wing which is strongly radiately striate and lightly reticulate, much broader at ends where rounded, their edges sometimes minutely jagged, the seed part up to 3.5 cm. long and 2.5 cm. broad, the wing up to 2.2 cm. long and 2.5 cm. broad at both ends, with margins near middle up to about 0.5 cm. broad, the albumen very thin, the cotyledons ovate, very thin and difficult to separate, up to 2 cm. long and 1.2 cm. broad, the radicle short; germination epigeal.

Type species.—*Dyera costulata* (Miquel) Hook. f.

Illustrations.—*Dyera costulata* (115): flowering branchlets; fallen leaf with gland adhering to petiole; mature flower-bud; corolla from expanded flower, and flower analyses; dehiscing follicle; seeds; stages in germination of seed. Four photos between pp. 110 and 111 (47): habit of a large tree; branch with inflorescences, fruit, and leaves; trunk of a large tree; close-up of bark. Getah Jelutong (98, pl. 3): habit photo of tree in Botanic Gardens, Singapore. (98, pl. 4): branch with leaves and flowers; flower analysis; fruit. *Dyera costulata* & *D. laxiflora* (17, pls. 19 & 20): habit, bole, leaves, and fruits (fide Symington). *Dyera laxiflora*, the big Jelutong Tree (15, p. 33): Habit photo of a large tree in the Singapore Bot. Gd. Fig. 4 (91): branches with leaves. “*Dyera costulata* Hoch.” (22, pl. 74): transverse & tangential sections (100×) and transverse section (10×). *Dyera Lowii* Hook. f. (6): tangential wood-section. *Dyera Lowii* (45): wood anatomy. Map 2 (72, p. 80): areas in the East Indies and Malaya in which Jelutong is extracted.

In addition to the published illustrations cited above, there are available in the Conservatoire et Jardin Botanique, Geneva, unpublished excellent line sketches showing detailed floral analyses, inflorescences, fruits, and leaves of *Dyera costulata* (under *D. costulata*, Maingay 1097 from Malacca, and Griffih from Malacca; Comm. Van Romburgh 1882 cult. in hort. bot. Bogar., Sumatra; also under *D. laxiflora*, coll. not cited). Del. Nov. 1902, E. Delpy; these drawings were from the herbarium of Charles-Joseph Pitard-Briau.

Field observations (see Cultivation and Distribution for further information).—*Dyera* in the forest has a predominance in the topmost story. The mature trees are usually so distinctive in appearance that they are rarely confused with other genera. The young plants, however, are sometimes mistaken for the closely allied Pulai (*Alstonia* spp.). Foxworthy (47, p. 110), referring to his experience with *D. costulata* in the Malay Peninsula, writes:

"Bark of saplings smooth, with horizontal markings indicating where leaves have fallen. As the young tree grows the bark acquires a curious reticulate pattern and shows a good deal of chlorophyll. This curious marking is lost before the tree reaches commercial size and the bark becomes rather smooth again. Trees growing in the open usually have a much lighter-coloured bark than those growing in dense forest."

Jelutong is very resistant to injury, girdling, burning, is very tenacious of life, and can grow through Lalang. It has a fair amount of natural regeneration.

*Dyera costulata* was observed by Holttum at Singapore as a deciduous tree or as intermediate between the normal deciduous and evergreen types, with no strictly regular leaf periods. There were complete leaf-changes at intervals of from 3 to 11 months, sometimes with partial changes in between; usually all the old leaves were lost before the new buds opened, but new leaves sometimes appeared before the old leaves had fallen. The tendency of leaf-fall was to follow dry weather. "Dyera trees," Holttum writes, "are fairly frequent in the Garden Jungle, and they tend to change their leaves at the same time, though they do not always behave alike." There are known some irregularities of behaviour, and all the trees do not always change their leaves simultaneously. Derry (29, p. 245) writes from his experience at Singapore: "The leaf-fall is usually complete, the tree entirely defoliating itself in a remarkable short space of time and is immediately followed by young leaves and flowers (about the end of March). The fruits ripen during the following February." Foxworthy (47, p. 112) states concerning Dyera in the Malay Peninsula that individual trees have been known to shed their leaves twice within one year. The new leaves have a bronze colour for the first few days while they are unfolding.

Foxworthy (47, p. 112) offers his observations on the flowering and fruiting habit of Dyera in the Malay Peninsula: "Flowering takes place within a few weeks after the appearance of the new leaves. Jelutong has been collected in flower in all months except January and December, and in fruit in all months except August. The flowers open at night or in the early morning and the corollas are usually shed before 9 A.M. There is a succession of flushes of flowers for about ten days and the amount of flowers borne is so great that the ground under the trees is each morning carpeted with the white fallen corollas, which turn brown within a few hours. The fruit is usually ripe within two or three months of the first appearance of the flowers. The seeds are dropped in the morning and are dispersed by the wind."

Watson (127, p. 57) writes that Dyera has no definite fruiting season in the Malay Peninsula. The fruits are estimated by him to take about two months to ripen. But Holttum (63, p. 190) asserts that the fruits of Dyera take nine months to ripen, although grown approximately full size in less than half that time. It is recorded that in Singapore they began to dehisce

about December 20th in 1929. Watson (127, p. 58) states that the opening of the follicles usually occurs in the afternoon, and is inhibited by dull or wet weather. The fruits do not fall until all the seeds have been released.

Ridley (106, p. 129) has observed seeds of *Dyera* blown by a fairly strong wind a distance of 40 yards from a tree 80 feet tall in the Singapore Botanic Gardens. He notes: "The tree sometimes attains a height of 200 feet and I have little doubt that the seeds are often blown to a much greater distance."

In reference to the seedlings of *Dyera*, Foxworthy (47, p. 111) states: "The first leaves are opposite and the whorled arrangement does not appear until quite a number of months have elapsed. The first four or five pairs of leaves are narrow, acute, much smaller than those of the mature tree, and are not noticeably glaucous beneath. They somewhat resemble in appearance the leaves of *Tembusu* [*Fagraea* sp.]. Later leaves are longer than those of the mature trees, sharp-pointed and glaucous beneath. They are followed by whorled leaves."

*Distribution.*—*Dyera* is common on the whole Malay Peninsula up to Penang and lower Siam (Püket).<sup>7</sup> Extending south to Malacca, it is known from the islands of Singapore, Riouw, Lingga, Singkep, Banka, and Billiton. *Dyera* occupies vast areas in Sumatra. It is very frequent in Sarawak and is widely distributed in Dutch and British Borneo and Brunei. Van Steenis lists the genus as questionably from Celebes.

*Dyera* grows in a variety of soils from low lying swamps with water one meter deep, or in flat or undulating lands, to dry hills up to 870 m. in altitude. It is not gregarious in primeval forests but is associated with various other genera. Principally a light demanding tree (Watson, 127, p. 59, states: "There is no doubt that Jelutong is a marked light demander"), it responds quickly to the opening of the forest canopy and it is believed that the silvicultural operations being undertaken chiefly in the interest of Dipterocarps will result in a very considerable increase in the proportion of Jelutong.

Foxworthy (47, p. 109) writes that *Dyera* in the Malay Peninsula "occurs

<sup>7</sup> *Dyera* is not reported from Siam in H. N. Ridley's Flora of Lower Siam and An Account of a Botanical Expedition to Lower Siam or in W. G. Craib's Contributions to the Flora of Siam (Year 1912). Ridley remarks (104, pp. 15, 55) on how the flora of lower Siam is "quite distinct from that of the Malay Peninsula," and notes (p. 59) *Dyera* as seeming to stop altogether south of Alor Star (Kedah). Kerr, in editing Craib's *Florae Siamesis Enumeratio* (27), cites two collections from Setul. These collections have been checked by me. It seems, then, that although *Dyera* is not altogether lacking from lower Siam, it is not widely distributed far north of the Federated States.

*Dyera* is known from the Ranau region in south Sumatra, but apparently fails to cross the Sunda Straits into Java. The genus is not found in Java, except in cultivation. Van Steenis (123, p. 37) notes *Dyera* not crossing the Sunda Straits and explains that: "the lowland forests of Sumatra, the Malay Peninsula, Borneo and the Philippines show a very close affinity, the typical representatives of which do not occur in Java and the Lesser Soluda Islands."

There is no record available of *Dyera* extending into the Andaman Islands or otherwise west of Malaya and Sumatra. East of Borneo there is only a dubious report of the genus from Celebes.

on flat land and low hills, from sea level up to about 1400 ft., on laterite or alluvial soil. Never the most abundant tree and, if the forests of the whole Peninsula are considered, it is doubtful if there is an average of more than one tree of commercial size to nine acres." It is listed as nineteenth in order of abundance amongst the more common commercial trees. Although distributed in every district, Dyera grows sporadically and is uncommon in the Malay Peninsula except on the lower lying hill forests.

Cantley in 1883 observed Dyera as on the road to extinction in Singapore Island. Brown (13) reports it is plentiful on the foot hills and low lying districts of the north, northeastern or eastern part of Singkep; that in the west of Lingga only a few trees are found on the foothills, but it is distributed on all low lying areas (4 or 5 trees per acre around Kotadaik and along the river Nereheh).

In Palembang, Sumatra, where areas have been cleared of other trees, Dyera is estimated (12) to be represented by about 8-10 large specimens per acre and as many young ones.

Jelutong is more densely distributed in certain areas in Sarawak and in the Netherland East Indies than in the Malay Peninsula. It is the most obvious tree in many swampy districts of the lower river basins, so characteristic that such areas are commonly referred to as "Jelutong Swamps." These swamps vary in width from 10 to 60 or more miles along the coast. They are not salty, brakish or stagnant. The soil is generally sandy; the forest, evergreen. The best areas are reported by Corson (26, p. 47) to have about 12 trees over 45 cm. diam. per acre. Dyera trees in the "Pantoengbosch," according to Heyne (59, pp. 42 & 51) generally stand at distances of 50 to 400 m. from each other. A survey for 1944 reports Dyera in the Pontianak region in Dutch Borneo is exhausted. Endert notes Dyera as one of the less common trees in the tuff plateau forests near Poehoes and L. Djenéau.

From a survey of literature and the collections examined, it seems that only *D. costulata* (including *D. laxiflora*) is known from the Malay Peninsula and Singapore. Both *D. costulata* and *D. Lowii* are found in all the other major regions. According to Brown (13), while *D. Lowii* is met in all the low lying swamps of Singkep and Lingga, *D. costulata* is restricted almost exclusively to the north and eastern districts of Singkep, although a few specimens of this species were seen in the foothills north of Lingga. Of these two islands, as far as *D. costulata* is concerned, Singkep is the only one worth exploitation. Smith (114, p. 307), on the authority of Drees, states that the habitat of *D. costulata* is dry lands at altitudes up to about 2600 feet, while that of *D. Lowii* is marshlands below an altitude of some 170 feet. *D. costulata*, Brown (12) claims, is exclusively a dry land species in Palembang. Specimens of *D. Lowii* grow much closer together in the jungle than those

of *D. costulata*, it is reported, but in the swamp habitat of the former species the undergrowth is thicker and travel from tree to tree is more difficult.

*Taxonomic relationship.*—In reference to the relationship of *Dyera*<sup>8</sup> to other genera, Hooker (67, p. 292) writes: "Its nearest affinity is no doubt with *Alstonia*, from which it differs conspicuously in the sessile stigma, a character rare in the Order, and in the singular fruit. It further differs from that genus in the extraordinary minuteness of the flowers, which are scarcely  $1/18$  of an inch in length, whilst the ovules have a diameter (as taken from dried specimens after saturation with warm water) of only  $1/200$  to  $1/300$  of an inch. These latter minute organs are succeeded by fruits of unusually large dimensions for the Order."

The close tie between *Alstonia* and *Dyera* is universally accepted. Schumann places *Dyera* in "Plumieroideae-Plumiereae-Alstoniinae." The floral and fruit or seed characters of *Dyera* easily distinguish it from all the other genera in this subsection. It should be noted that there are other members in this group with winged seeds, but the precise morphology of their seeds is obviously different. Considering the gross features of *Jelutong*, its tree habit removes it from the genera numbered 36-44 in Schumann's treatment, which are either vines or subshrubs (the West Indian *Strempeliopsis*, sometimes arborescent, seeds winged, has its leaves minutely finely lineate and an entirely different appearance from *Dyera*). The fruit bears no resemblance to those in the genera numbered 32-35. The leaves of *Plumeria* (fruit large follicles, seeds winged) and *Stephanostegia* are spirally arranged. In *Skytanthus* and *Holarrhena* the leaves are opposite; the former genus has its anthers with characteristic long tail-like appendages at their apices, the latter has its linear-fusiform seeds comose at one end. *Gonioma*, from the Cape, has whorled leaves, but is a shrub with an entirely different aspect from *Dyera*, in addition to having various technical differences (e.g., ovules in 2 ranks, style long).

The resemblance between *Dyera* and the remaining two genera, which immediately precede it in Schumann's treatment, is highly significant. *Paralstonia* has its seeds somewhat winged but the thickened follicles are short, little surpassing the length of the seeds; the ovules are in two series; the anthers are without the fleshy appendage so characteristic in *Dyera*; the flowers are arranged in fascicles in the inflorescence-branches.

In view of the obvious similarity both technical and habitat between *Dyera* and *Alstonia*, the great amplitude of sectional heterogeneity within the latter genus and the wide diversification of its forty or more species, compared with the almost monotypic character of *Dyera*, it might be argued that *Dyera* is merely a limital representative of *Alstonia*, in which it might be best included. In my judgment, however, *Dyera* is sufficiently distinctive

<sup>8</sup> The genus was named in honor of W. T. Thiselton-Dyer.

to be maintained in its generic status. The two genera are compared<sup>9</sup> by the following key (italics) and descriptive characters:

Trees, glabrous, the branchlets stout; leaves whorled; gland at axil of petiole conspicuous large rigid; *inflorescences axillary* at base of season's new growth; flowers glabrous except for ring of hairs within corolla-tube below stamens; *calyx-lobes glandular* at base within; corolla-tube very short, naked at throat; corolla-lobes overlapping to right; stamens inserted a little below middle of corolla-tube; *anthers with connectives produced into a large thickened fleshy appendage*; ovary pubescent, half or more inferior; *style very short, indistinct*; gland surrounding ovary apparently none; *follicles very large and thick*; *seeds large, membranous-winged, glabrous*. . . . . *Dyera*. Trees to shrubs, glabrous to pubescent, the branchlets stout to slender; leaves whorled or opposite; gland at axil of petiole not as conspicuous as in *Dyera*; *inflorescences apparently terminal*; flowers glabrous to pubescent; *calyx usually eglandular*; corolla-tube very short to long, without or with a ring at throat; corolla-lobes overlapping to right or left; stamens inserted from near middle to almost throat of corolla-tube; *anthers without thickened appendage*; ovary pubescent to glabrous, half inferior to entirely superior; *style filiform, distinct*; disc apparently none, or annular, lobed or truncate; *follicles slender*; *seeds relatively small, comose or ciliate, not winged*. . . . . *Alstonia*.

The species of *Dyera* are very closely interrelated, having overlapping vegetative characters and hardly any floral differences. "The species are so difficult to distinguish," wrote Burkhill (16, p. 875), "that it is impossible to assign much of the available information to any one." This author, however, might have had in mind only the Malayan plants, *D. costulata* and *D. laxiflora*, which are here accepted as representing a single taxonomic unit. Ridley (99, p. 191) states: "I am rather doubtful as to whether there is really more than one variable species of the genus." Nevertheless, he (94, p. 249) found *Haviland 2170* (which is *D. Lowii*) a "very distinct plant." Romburgh (108, pp. 23 & 153) claims that various examples of Djeloetoeng he had observed in the jungles of Borneo resembled entirely or seemed identical in all parts, leaves, flowers and fruits, with *D. costulata* which he examined in the Botanical Gardens at Pontianak and Singapore. Howes remarks that there does not appear to be any intrinsic difference in the Jelutong of the three species, *D. Lowii*, *D. costulata* and *D. laxiflora*, though the Malayan product, owing to better methods of preparation, is generally preferred and commands an enhanced price. It is doubtful, Derry (28, p. 51) opined, whether the Jelutong produced by *D. Lowii* [spelled "*Dyera Lowiana*" through error] is distinct from that of *D. costulata*.

The taxonomic differences between the only two acceptable species of *Dyera*, *D. costulata* and *D. Lowii*, are extremely tenuous and difficult to express as key characters. I emphasize that it is highly dubious whether *D. Lowii* merits specific separation from *D. costulata*. Their practical differentiation, if any, must rely chiefly upon actual comparative experience. The most reliable judgment in specific identification here is that based on the agreement of several features, allowing any one of these features a wide

<sup>9</sup> The characters submitted for *Alstonia* are derived from literature and a very limited personal experience with the genus; consequently they are tentative. A taxonomic revision of *Alstonia* by the writer is proposed for the near future.

amplitude of individual variation. There is no clear delimitation for any single character and sometimes several or all the diagnostic features of the two species seem to intergrade. Obviously, the difficulty in naming incomplete or scanty herbarium material of non-typical specimens is sometimes insurmountable.

Leaf-blades (typical) rounded to subcordate, or narrowed but finally lightly rounded at base, short-acuminate to rounded at apex; anthers oblong-lanceolate, abruptly acute or obtuse at apex below the mucro, 0.99–1.26 mm. long.....*D. costulata*. Leaf-blades (typical) cuneate-narrowed at base and decurrent on petiole, rounded at apex, the principal lateral nerves more numerous and closer together than in *D. costulata*; calyx-lobes tending to be more acute; anthers lanceolate, gradually acuminate at apex and merging into the mucro, 1.26–1.58 mm. long (only buds examined).....*D. Lowii*.

Seeds of only a single specimen of each species were examined; those (matured?) of *D. Lowii* were merely up to 3.5 cm. long and 1.3 cm. broad, whereas those of *D. costulata* were up to 7 cm. long and 3 cm. broad. *D. Lowii* is reported by Brown to have pneumatophores, whereas aerial roots are lacking in *D. costulata*. It is said not to grow as large as *D. costulata*, with bark not so thick, and the latex not so viscous or abundant. Brown adds, moreover, that *D. Lowii* is not so liable to disease as *D. costulata*. Several authorities agree that *D. Lowii* inhabits damp swampy lands below 50 m. alt., whereas *D. costulata* prefers dry hill forests up to 800 m. alt. In reference to altitudinal distribution, however, there are available typical specimens of *D. costulata* collected on terrain less than 20 m. high (as low as 5 m.).

In reference to the important feature of pneumatophores Romburgh (108, p. 153) states: "Dans les forêts humides où le sol est inondé de temps, on distingue déjà à une assez grande distance la présence de cet arbre grâce à certains renflements (souvent plus gros qu'une tête d'homme) que portent ses racines superficielles. L'écorce de ces renflements est d'un brun jaune, riche en latex, et couverte de lenticelles.—Dans les terrains plus élevés et plus secs, ces tubérosités sont complètement défaut."

I. *DYERA COSTULATA* (Miquel) Hook. f., Jour. Lin. Soc. Bot. 19: 293.  
Aug., 1882.

*Alstonia? costulata* Miquel, Fl. Ind. Bat. Suppl. 556. 1860.

?*Alstonia eximia* Miquel, loc. cit. 555.

?*Alstonia grandifolia* Miquel, loc. cit. 555.

*Dyera laxiflora* Hook. f., Fl. Brit. India 3: 644. Dec., 1882.

Type of *Alstonia?* *costulata*.—"Sumatra occid. in prov. Priaman (*Diepenhorst*)."  
This collection consists of sterile material.

Hooker, under his original publication of *Dyera costulata*, cites: "Hab. Sumatra, Teysmann; Malacca, Griffith, Maingay (Kew distrib. 2573)." The Teysmann collection consisted of foliage only; the Griffith specimen was in flower, and the Maingay plant included flowers and fruits. As a

Malacca plant of *D. costulata*, Hooker also mentions a specimen collected by "Murton, late Superintendent of the Singapore Botanical Gardens, who has communicated to the museum at Kew leaves and old fruits, from which unfortunately the seeds have escaped." In this connection, it should be noted that a *Murton* specimen from Singapore was subsequently selected as a cotype of *D. laxiflora* Hook. f. King & Gamble cite for *D. costulata*: "Sumatra (Teysmann, Diepenhorst 1114)."

*Distribution.*—*D. costulata* is found generally in the entire range of the genus. It is the exclusive species in the Malay Peninsula.

*Specimens examined.*—Siam, Setul: *Kerr* 13909 (Tung Wa; fl., Jan.; A, K, P); *Lakshnakava* 353 (fl. & fr., Nov.; K, P). Federated Malay States: *For. Dept. F.M.S.* 1772 (Kuala Lumpur; fl., Oct.; K), 2258 (Selangor; fr., Nov.; K), 3328 (Kuala Lumpur; immature fl., April; K), 3391 (Pulau Penang; immature fl., June; K), 3885 (Kuala Lumpur; fl. past anth., June; K), 4906 (Foxworthy; Kuala Lumpur; fl. past anth., Sept.; K), 4917 (Kuala Lumpur; fl. past anth., Sept.; K); *Griffith s.n.* (1845; K); *King's Coll.* 4689 (Larut, Perak<sup>10</sup>; fr., Aug.; K), 7852 (Perak; fl., July; K); *Maingay* 1097 (=No. 2573; Malacca; fr. & fl., Aug.; K); *Scortechini* 1973 (Goping; K) *Wray* 541 (fr., Jan.; Perak; K). Singapore: *Anderson* 119 (K); *Burbidge s.n.* (Year 1878; K); *Cantley* 226 (1882; cotype coll. *D. laxiflora*; fl., Aug.; G, K); *Clemens* 22455 (fl., Oct.; N.Y.); *Hullett* 343 (K); *Nas s.n.* (fl., Oct.; A, NY); *Ridley* (1890; K); *undesig. coll.* (1882; K). Riouw; *Neth. Ind. For. Ser.* 29993 (en Ond. Indragirische-bovenlanden, Moeara Serange; M). Sumatra: *Castillo & Valderrama* 10 (Palembang; C, K); *Endert*. 37 E. 1 P. 466 & 38 E. 1 P. 394 (Palembang; K, P); *Krukkoff* 237 (West Coast, Hoeta Padang Estate, near Kisarin; NY); *Neth. Ind. For. Serv.* 16400 & 16407 (East Coast, below Langkat; A), 31601 (East Coast, Serdang Boschreserve Silinda; A); *Teysmann s.n.* (ex herb. Miquel; K). Sarawak, Borneo: *Clemens* 21502 (Gat, upper Rejang Rv.; A); *Haviland* 2049 (path to Teyora; fl., Dec.; K). British North Borneo: *Ramos* 1912 (Sandakan or vicinity; fr., Sept.—Dec.; A, P, US); *D. D. Wood* 2290 (C). Dutch Borneo: *Neth. Ind. For. Serv.* 16255 & 16265 & 16280 & 16742 & 16962 (southeast division, West. Koetei; A), 17952 & 18246 (south-east division, Tidoengsche Landen; A), 21178 (south-east division, Poeroek Tjahoe Tahoedjan; A), 24663 (south-east division, West. Koetei; A); *Winkler* 2435 (south-east division, Hayoep; K). Hort. Bot. Bog., Java: *Merrill s.n.* (fr., Nov.; cult; NY, US); *undesig. coll.* 359 (cult; US). Hort. Bot. Reg. Kew, England: *Holland s.n.* (det. doubtful; cult., undesig. origin; K).<sup>11</sup>

The type of *Alstonia eximia* was from "Bangka, prope Djebus (Teysmann)" and that of *A. grandifolia*<sup>12</sup> was from "Sumatra orient. in prov. Palembang (Teysmann)." These two species were described from sterile material (*A. grandifolia* in fruit). The diagnoses are in harmony with *Dyera costulata*, although too incomplete for positive identification. The follicles of *A. grandifolia* are described as elongated and woody, which is the fruit character of *Dyera* rather than *Alstonia*. The apiculate leaf-apices in the two plants suggest *D. costulata* rather than *D. Lowii*. Miquel states

<sup>10</sup> 4689 is cited by Narayanaswami as collected by Kunstler in Gopeng.

<sup>11</sup> This specimen is sterile, consisting of a branch with terminal leaves. The leaf-blades have their lateral nerves more numerous (up to 25 principal pairs) and closer together (mostly 5–7 mm. apart near middle) than is usual in *D. costulata*; they are slightly retuse at the apex and acute-decurrent at the base. The only information appearing on the label is: "From Mr. Holland, 1916. Herb. Hort. Bot. Reg. Kew. Dyera laxiflora, H.K. f. det. J. Hutchinson. 23.6.1916." Its anomalous appearance may be accounted for by the growth of the plant under artificial conditions.

<sup>12</sup> *A. grandifolia* is cited in Catalogus Plantarum quae in Horto Botanico Bogoriensi Coluntur (1866).

that *A. grandifolia* approximates *A. eximia*, but is more robust and with larger leaves. In the absence of the actual specimens, I place these species questionably in synonymy of *D. costulata*, where they very probably belong.

The above disposition of *A. eximia* and *A. grandifolia* is in agreement with that of Heyne (60, p. 1276) and Symington. Heyne cited these species as belonging to Dyera: "*Alstonia (Dyera) Eximia* Miq." and "*Alstonia (Dyera) grandifolia* Miq." For the former he stated: "De onder dien naam beschreven boom behoort echter tot het geslacht Dyera"; and for the latter: "Ook deze boom is ongetwijfeld een Dyera soort en zeer waarschijnlijk identiek met *D. costulata* Hook. f." Hooker (68, p. 643) describes *A. grandifolia* under Species of Doubtful Position, and cites *T. Anderson* (Singapore). He notes: "Of this I have seen only two leaves, which precisely agree with Miquel's from Sumatra." Likewise, King & Gamble place *A. grandifolia* under Species Imperfectly Known and cite *Anderson* 119. Ridley (105, p. 348) states that the *Anderson* collection consists of leaves apparently of *Dyera costulata*; Symington also identifies them as of *D. costulata*, and there is no doubt that this determination is correct.

The cotypes of *Dyera laxiflora* Hook. f. are: "Singapore; Murton, Cantley." The following is the original description of this species by Hooker: "leaves narrowed to the rounded or subacute base, cymes long peduncled, corolla-lobes four times as long as the tube. Closely allied to *D. costulata*, but with much larger leaves, sometimes 8 in. long, petioles  $1\frac{1}{2}$ -2 in. Peduncles of cymes very slender, 3-5 in., pedicels  $\frac{1}{4}$ - $\frac{1}{2}$  in. Corolla-lobes linear,  $\frac{1}{3}$  in. long." In comparison, Hooker notes in the same work the following characters for *D. costulata*: leaves rounded at the base, 2-4 in. long, petioles  $\frac{1}{2}$ -1 in., cymes shortly peduncled, 2-3 in. long, pedicels short, corolla-lobes about twice as long as the tube.

King & Gamble, Ridley in the Flora of the Malay Peninsula (105, p. 345), and Foxworthy (47, p. 110) accept the validity<sup>13</sup> of *D. laxiflora* and compare it with *D. costulata* as follows (characters compiled from the three works conjointly):

Corolla-tube (0.075 in. long) much shorter than lobes (0.2 in. long); cymes with long peduncles; fruits rather larger than in *D. costulata*, seeds distinctly smaller (about 2 in. long and not more than  $\frac{3}{4}$  in. wide including wing); leaves under 8 in. long, shorter acute at tip, the main lateral

<sup>13</sup> Mention has already been made of Ridley's expression of doubt in the Agricultural Bulletin (99, p. 191) concerning the validity of *D. laxiflora* & *D. Lowii* as distinct species from *D. costulata*. Previously in the same Bulletin (98, p. 95) Ridley had gone on record as regarding *D. costulata* and *D. laxiflora* synonymous. Several years earlier (Year 1900, 94, p. 249) he had written: "The leaves vary a good deal and are often smaller than described and in young shoots, stumps, etc., very much longer. This variation in specimens is perhaps the cause of two species of Dyera being described in the Flora of British Indies, viz. *D. costulata* and *D. laxiflora*. I have not recognized more than one species here, but the Malays do talk of two plants, Jelutong and Jelutong Pipit."

nerves (13–17 pairs) starting at about  $60^{\circ}$  with the midrib.....*D. laxiflora*.  
Corolla-tube (0.1 in. long) nearly as long as lobes (0.15 in. long); cymes with short peduncles;  
leaves usually under 6 in. long, the main lateral nerves (16–20 pairs) starting nearly at right angles  
to the midrib.....*D. costulata*.

According to Foxworthy, *D. laxiflora* has a denser crown than *D. costulata*; bark thicker, with rougher surface, inner bark rather whitish (pale brownish in *D. costulata*); latex much less. According to Burn-Murdoch, *D. laxiflora* yields about  $\frac{1}{5}$  as much latex as *D. costulata* (*D. laxiflora* yields practically no Djeloetoeng, according to Heyne, Recueil, p. 52); wood is lighter (19.5 lb. per cubic ft.); and the tree is more common than *D. costulata* in the Malay Peninsula.

Several other authorities apparently have accepted the validity of *D. laxiflora*, but the latest and most thorough student of the problem, Symington, finds this species identical with *D. costulata*. Watson (127, p. 57) writes concerning *D. laxiflora*: "As a result of careful examination by the Forest Botanist of the type material on which the descriptions were based, combined with field investigations, which have been greatly facilitated by the large number of trees now being tapped all over the country, there is hardly room for doubt that the second species can not stand." Burkill (16, pp. 875 & 876) makes a similar statement. And in his own words, Symington concludes: "After study of the herbarium material at Kew, Singapore, and Kepong, and after considerable field observation, I am forced to conclude that we have but one species [in the Malay Peninsula], namely *Dyera costulata* Hook. f."

I have examined a fair representation of the two species, including a cotype of *D. laxiflora*, and besides finding the flower-pedicels in the latter to average a trifle longer than in typical *D. costulata* I could not discover any difference between the two. This apparent difference in length of pedicels is hardly uniform even in equally matured flowers and is not without intergradation even in the very limited material examined by me; consequently it should not be regarded as of specific value.

Naturally, as it is true of most of the economically important plants which have been extensively exploited, there are recognized in *D. costulata* various minor field distinctions which are sometimes based on real individual or local (ecological) variations. Generally, however, the popular classifications fancied by the native collectors of latex are mere chimeras. Brown reports that some individual trees have a different type of bark from others—thin hard bark, and produce less latex than those whose bark is thick and quite soft. Foxworthy (47, p. 111) also notes that some individuals are very much better yielders than others. Burkill (16, p. 876) states: "Collectors of latex frequently distinguish between red-barked and black-barked kinds, but, so far, no one has succeeded in definitely rec-

onciling any particular forest characteristics with either of the two supposed forms. Their requirements in the way of soil appear to be identical."

2. DYERA LOWII Hook. f., Jour. Lin. Soc. Bot. 19: 293. Aug., 1882.

?*Alstonia polyphylla* Miquel, Fl. Ind. Bat. Suppl. 556. 1860.

*Dyera borneensis* Baillon, Bull. Men. Soc. Linn. Paris 1(94): 751. 1888.

*Cotypes of D. Lowii*.—"Hab. Borneo, Low, Beccari; Sarawak, Thos. Lobb." The Beccari specimen is numbered 3570.<sup>14</sup>

Hooker notes that he also examined a flowering specimen collected by Burbidge from cultivation in the Singapore Botanical Gardens. The only Burbidge collection seen by me is of *D. costulata*; it is deposited at Kew and is probably the specimen Hooker had in mind.

*Distribution*.—*D. Lowii* is found generally in the entire range of the genus outside of the Malay Peninsula. It is reported from Borneo and Sumatra, and Billiton, Banka, Singkep, Lingga and Riouw.

*Specimens examined*.—Riouw: *Neth. Ind. For. Serv.* 28564 (en Ond. Indragirische-bovenlanden, Belimbang; A), 29145 (en Ond. Indragirische-bovenlanden, P. Gelang; M). Billiton: *Heyne* 765 (K). Dutch Borneo: *Low s.n.* (cotype; K); *Neth. Ind. For. Serv.* 18112 (south-east division, Koeala Kapoeas; A), 19973 (south-east division, Benede Dajak, Bawan; A). British North Borneo: *J. P. Edwards* 3893 & 3894 (Mile 53: J'ton-B'fort; K). Sarawak: *Beccari* 3570 (type of *D. borneensis*, cotype *D. Lowii*; K, P); *Haviland* 2170 (Kuching; fl., Dec.; K); *Haviland & C. Hose* 3495 (Niah; fl. & fr., May; K); *Thos. Lobb s.n.* (1857; cotype; K).

The type of *Alstonia polyphylla* is from "Bangka (Teysmann)." The species was described from sterile material. The diagnosis is in harmony with *Dyera Lowii*, although too incomplete for positive identification. The leaves cuneate obovate or obovate-oblong, broadly rounded or sometimes retuse at the apex, suggest *D. Lowii* rather than *D. costulata*. In the absence of the actual specimen, I place this species questionably in synonymy of *D. Lowii*. It should be noted that the publication of *A. polyphylla* antedates that of *D. Lowii*, and in the event the two are proven identical, which most probably will be the case if the type of Miquel's species becomes available, *D. Lowii* (unless conserved) will fall into synonymy under *Dyera polyphylla*.

Heyne (60, p. 1277) referred *A. polyphylla* to Dyera with certainty: "*Alstonia (Dyera) polyphylla* Miq. . . . De door Miquel beschreven plant is zeker een Dyerasoort een gelijkt zeer op *Dyera Lowii* Hook. f."

The type of *Dyera borneensis* is from Sarawak, Borneo, "le N° 3570 de la collection Beccari." It was extracted from the cotypes of *D. Lowii*, published earlier by Hooker. Baillon, in Bull. Soc. Lin. Paris, states that he believes *Beccari* 3570 is a Dyera. In which case, he adds, some modifications are desirable in Hooker's generic diagnosis: the ovary is  $\frac{1}{2}$ – $\frac{2}{3}$  inferior, its two cells incompletely closed at the top, the thecae of its anthers very

<sup>14</sup> *Beccari* 3570 was subsequently selected by Baillon as the type of *Dyera borneensis*.

unequal. These characters are repeated by Baillon in the generic description of *Dyera* in *Histoire des Plantes*. Baillon adduces hardly any specific features for distinguishing *D. borneensis*. The leaf-blades of *Beccari* 3570 are noted as being attenuated at base, rounded at apex, and with at least 20 pairs of secondary nerves.

I find the ovary in *Dyera* to be partly inferior as noted by Baillon, but consisting of two very closely set carpels. There is thus no indication of a single cell. Schumann remarked that he doubted *D. borneensis* was a *Dyera*, judging by its supposed one celled ovary.

Burkill (16, p. 875) stated that *D. borneensis* and *D. Lowii* are probably identical and, moreover, perhaps identical with *Alstonia polyphylla*.

I have examined the type collection of *D. borneensis* and do not hesitate to place the species with the typical material of *D. Lowii*.

#### EXCLUDED NAMES

"*Dyera Maingayi* Hook. f."—nomen nudum. Ridley, in Malay Plant Names (Year 1897. 93, p. 110) lists *Dyera Maingayi* Hook. fil. and *D. costulata* Hook. fil. as corresponding to the native name Jelutong. He submits no description for either name, merely remarking: "A big tree which gives a very inferior India Rubber, and a timber used for clogs, boxes and such things." The name *Dyera Maingayi* has appeared without diagnosis in the works of various other authors: Morris (year 1898), Warburg (1902), Ridley & Curtis (1902, As *D. Maingayii*), Skeat & Blagen (1906). Said to abound in the Malay forests and noted to have a bark corresponding closely to the color of the Spectacled Monkey), Clercq (1909), Gerth van Wijk (1941. A Dictionary of Plant Names). The only original species of Apocynaceae described by Hooker fil. in The Flora of British India under the specific name *Maingayi* are in the genera *Vallaris*, *Urceola*, and *Epigynum*.

"*D. Plumosa*."—After referring to *Dyera costulata*, Derry (29, p. 51) adds in a footnote that another species, "*D. Plumosa*," grows in Fiji and is stated to produce rubber of some value. The name is probably an error for *Alstonia plumosa*. Jumelle (70, p. 168) records that, on the basis of a sample sent from Fiji and experimented upon at Kew, *Alstonia plumosa* produces a very useful caoutchouc.

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## Studies on Some Fungi of Northwestern Wyoming

### III. Pleospora and Leptosphaeria<sup>1</sup>

LEWIS E. WEHMEYER

A previous paper (10) was devoted to a general list and account of the fungous flora of northwestern Wyoming, and data concerning elevation and other particulars of the chief localities in which collections were made can be found therein. The present paper is concerned with a more detailed consideration of the many collections of the genera *Leptosphaeria* and *Pleospora* made upon herbaceous stems in this region.

The taxonomic situation in the genera *Leptosphaeria* and *Pleospora* is one of great confusion. This confusion stems from two sources; first the actual situation as it exists in nature; and second, that created by systematic mycologists in the literature. Let us look more closely at these two sources of confusion.

It is necessary to realize at the outset that nature recognizes no such entity as a species. There exists in nature a vast assemblage of individual occurrences which present an overlapping series of variations for almost any character one wishes to mention. Such a series for any one character, furthermore, is not necessarily correlated with the series for any other character. Only where long periods of time, or other factors, have eliminated blocks of such series, do well defined groups of individuals stand out as isolated entities which we can recognize as natural species. In other complexes, particularly if variation is actually taking place at the present time, specific lines must be drawn in an entirely artificial manner and all sorts of intergrades, which must be arbitrarily placed, are to be expected.

For example, if one takes a large series of collections, or even such a moderate number as in the present study, of *Pleospora*, and arranges them according to several spore characters such as size and septation, it will be found that over a wide range there are no breaks in the overlapping variations of individual collections. Where there are such breaks, one suspects and often finds that further collections will fill these gaps. A certain correlation will be found between spore size and septation, i.e. the smaller spores, in general, have the fewer septa, but here too there is a great deal of overlap. The greater the number of characters considered, the greater this apparent confusion becomes. This leads one to the concept of large species complexes, within which specific or varietal boundaries are purely arbitrary.

In such a situation it is obligatory that any exposition of the natural relationships should be based upon the careful comparative study of a

<sup>1</sup> Papers of the Department of Botany, University of Michigan No. 766.

large series of collections covering the entire field of the category under consideration. This has never been done for either *Pleospora* or *Leptosphaeria*.

What then is the present situation in the taxonomic literature? If one plots, as mentioned above, the spore size and septations as recorded in Saccardo for the various described species, the same overlapping series presents itself, suggesting that individual variations are being described as species. This, however, is only a superficial manifestation of several sources of confusion. Most species have been erected upon one or a few collections without any regard to their relation to the already described species or the plan of evolution within the group. Each individual worker has used his own concept of what character or characters are of diagnostic value, so that important data are often lacking in a description and there is an insufficient common background upon which the supposed species can be compared. The concept of the host occurrence as a differential character, for instance, is used by some writers and not by others. The present study indicates that species of *Pleospora* are not limited as to the host genus upon which they occur. A glance at the tables presented will show this. Nevertheless, the difficulty of matching collections with published descriptions has led species describers to accept the occurrence of a *Pleospora* on a new host as the basis for the erection of a new species. This naturally leads to numerous synonyms, which are, however, almost impossible to place correctly until the true relationships of these fungi as they exist in nature are known.

If one looks farther in the literature, another consequence of this confusion appears. Each writer has made his own interpretation of described species so that spore measurements and other characters show a wide variation in the interpretation of one and the same binomial in different publications. Many determinations, likewise, are unreliable. Another source of confusion is the fact, already mentioned (10), that several species, particularly of *Pleospora*, often occur intermixed on one and the same stem. As a result, even much type material consists of such mixtures.

From what has just been said, it is obvious that the application of binomials to collections of *Pleospora* and *Leptosphaeria* is a somewhat hazardous undertaking. In the following pages an attempt has been made to arrange a series of western collections of *Pleospora* and *Leptosphaeria* in such a way as to indicate the general tendencies in the evolution of these groups so that natural species groups based largely upon spore characters, which seem to be the most dependable, could be detected. When collections having a similar spore form are arranged according to spore size and septation it is found that the different series of overlapping spore sizes do show slight breaks which are sometimes correlated with change in spore form and sometimes not. These groups, which are rather large, for the most part, are

considered here as species. Such a conservative separation is believed by the writer to be the preliminary step in any recognition of natural species. Further study of larger numbers of collections may show other characters which may be used to segregate smaller groups as species or varieties, or may advise the union of groups now supposed to be good species, but to make such separations without sufficient data to show real differences is what has caused a great deal of the confusion in the past. The naming of these groupings is another matter. Most of the groups present ranges of variation which extend over that of several already described species. Ultimately, a name is merely a handle to be used as a convenience. If misused, it may equally become an inconvenience. When type material has been found to fall in these groups, the name applied to this type is used, or if a group seems to coincide with a commonly used name, it is also adopted. The probable change of these names in the future does not seriously worry the writer, if such change is proper and helps simplify the nomenclature. The important thing is to recognize the group of collections, present and future, which may properly go together to form a natural species or other group.

#### PLEOSPORA

The spore forms in both *Pleospora* and *Leptosphaeria* appear to be derived from a common type which is the 3-septate, dark brown, ellipsoid or inaequilateral spore common to many species of *Leptosphaeria*. In *Pleospora* the spore forms can be roughly grouped into four series. In the first, the spore is derived from the *Leptosphaeria* type just mentioned by the insertion of vertical walls in only some of the transverse cells, or in an irregular fashion. In the second, the vertical walls are more constant, but often absent from the end cells, but the spore retains the inaequilateral fusoid-ellipsoid form. In the third series, there is a greater tendency for the formation of vertical walls. There are often two, three or more vertical walls here formed in each transverse section. The end cells are usually vertically septate and the spore becomes broader, oblong-ellipsoid, with rounded ends. There is also a tendency for the spores to be asymmetrically divided, by a constriction, into two unequal portions. The fourth series, distinct from the first three in the flattened character of the spores, has been segregated into a separate and fairly distinct genus, *Clathrospora*, which is characteristic of high latitudes and altitudes. The perithecia in *Pleospora* are often thick walled or sclerotial and the development is probably of the pseudosphaeriaceous type throughout, but they may become thin-walled and in many species are pezizoidly collapsed. There is a definite tendency for the formation of a radiating brown tomentum from the base of the perithecium in many species, or of upright spine-like hyphae from the upper portion. This latter character has been used to segregate the

genus Pyrenophora. This character is sometimes quite pronounced, but there is so much variation with age and conditions of growth, that it is of doubtful value as a generic character. Other genera, such as Catharinia Comoclathris etc. have been segregated, but in this account all species are reported under Pleospora.

With the spore changes mentioned above, the asci in Pleospora tend to become broadly ellipsoid to saccate with thickened walls and a short claw-like base. There is, apparently, a thick gelatinous layer just inside an outer tough wall. At maturity, in water, this gelatinous layer absorbs water creating a pressure which ruptures the outer wall at some point (not necessarily the apex). When this occurs the protoplasmic content of the ascus elongates to twice or more the length of the ascus wall, carrying the spores within it in a single row, beyond the old and now discarded ascus wall. This emission of spores was seen in asci which had been dried in the herbarium for four years.

Only one species belonging to the first spore type was found in the Wyoming collections, and it appears to be new.

### Pleospora Amelanchieris sp. nov.

Pl. 1, Figs. 1-2

Perithecia large,  $400-800\mu$  in diameter, subglobose or slightly flattened, carbonaceous, black, rimosely cracked, ostiole not apparent or present as a mere perforation from which radiate deep cracks in the wall. Perithecia formed beneath the periderm, which tissue is, however, soon exfoliated, leaving the perithecia superficial and appearing as a Teichospora, thickly scattered or clustered, walls thick ( $50-100\mu$ ), of coarse black parenchyma.

Asci clavate at first, becoming long cylindric, with a claw-like base,  $140-195 \times 14-16\mu$ .

Spores biseriate at first, becoming uniseriate, oblong- to fusoid-ellipsoid,  $22-26 \times 9-10.5\mu$ . These spores are primarily 3-septate, but secondary transverse or vertical septa can be laid down in any or all of the central cells, giving rise to a 3-5 septate spore. The septa in the end cells are often oblique, forming a "Y"-shaped septum.

Hoback Canyon July 16, on *Amelanchier elliptica* A. Nels. legit L. E. Wehmeyer (1141) (Type).

Perithecia  $400-800\mu$  diametro, subglobosa vel paululum depressa, atra, dense dispersa vel aggregata, carbonacea, rimosa, sub peridermate mox exfolianti formata, delapsu peridermatis superficialia ut in Teichospora, parietibus  $50-100\mu$  crassis, atris, parenchymatosis; ascis clavatis,  $140-195\mu$  longis,  $14-16\mu$  crassis, ultimo longe cylindricis, basi unguiformibus; sporis biseriatis, demum uniseriatis, oblongis vel fusiformiter ellipsoideis,  $22-26\mu$  longis,  $9-10.5\mu$  crassis, primum triseptatis sed saepe septis secondariis transversis vel verticalibus in cellulis singulis vel in omnibus centralibus, ad ultimum 4- vel 5-septatis, septis in cellulis terminalibus obliquis Y-formibus.

Specimen typicum in ramis *Amelanchieris ellipticae* A. Nels., in Hoback Canyon, Jackson, Wyoming, 16 Jul., 1940, legit L. E. Wehmeyer, sub numero 1141.

This species is characterized by the large, black, rimose perithecia which

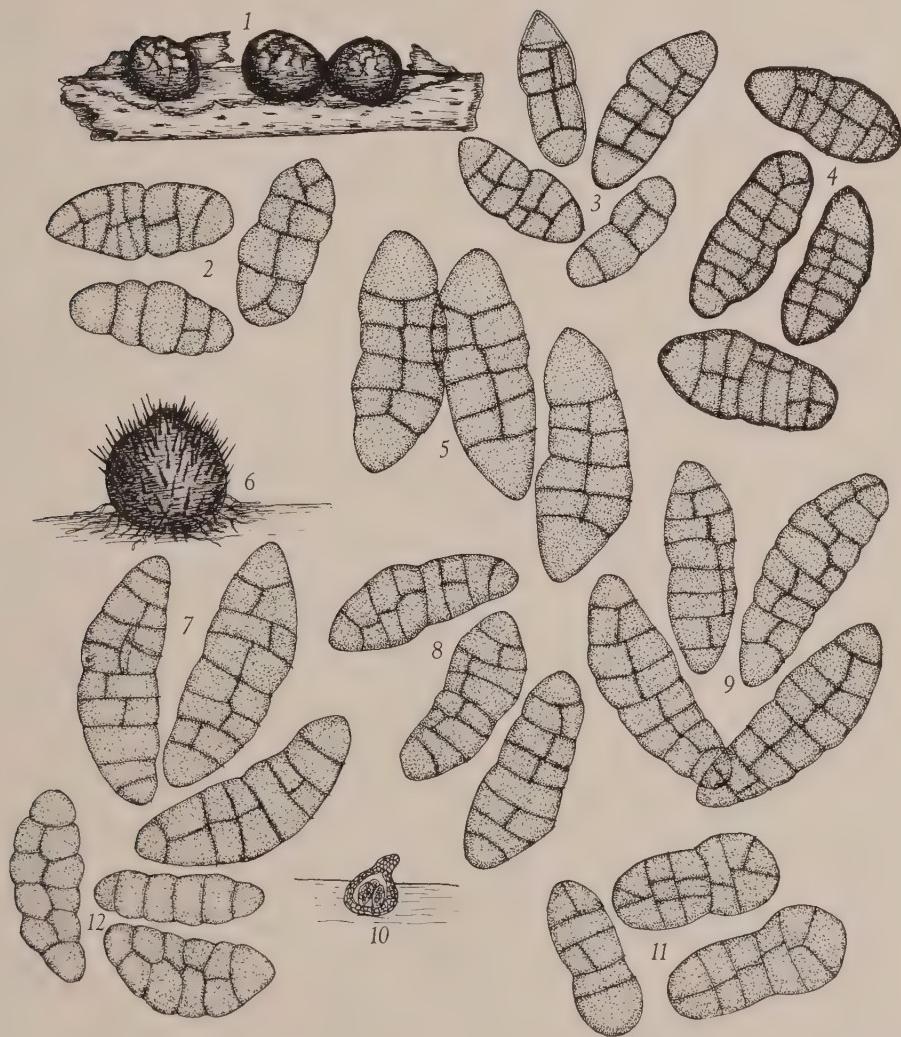


PLATE I. 1. Habit of "rimose" perithecia of *Pleospora Amelanchieris* sp. nov. 2. *Pleospora Amelanchieris* sp. nov. 3. *Pleospora vulgaris* Niessl. 4. *Pleospora Compositarum* Earle. 5. *Pleospora rictophensis* E. & E. 6. Setose perithecia of *Pleospora (Pyrenophora) pleosphaerioides* sp. nov. 7. *Pleospora (Pyrenophora) pleosphaerioides* sp. nov. 8. *Pleospora punctata* sp. nov. 9. *Pleospora (Pyrenophora) tomentosa* sp. nov. 10. Vertical section of perithecium of *Pleospora oligasca* Bub. 11. *Pleospora oligasca* Bub. 12. *Pleospora (Clathrospora) togwontiensis* sp. nov. Scale, 1 mm. = 1 $\mu$ . Figs. 1, 6, 10. Perithecia. Figs. 2-5, 7-9, 11-12. Ascospores.

soon become superficial by the exfoliation of the periderm, and by the variable septation of the spores. It has been issued by Clements (Crypt. Form. Colo. No. 456) as a new species, *Teichospora praestipa*, but, apparently, a description was never published. It might easily be mistaken for a Teichospora. It is near *P. Shepherdiae* Pk., but that species differs in the more deeply seated, not widely erumpent perithecia, whose surface is granular rather than rimose; in the narrower ( $110-160 \times 7-9\mu$ ) more cylindric ascii; and in the spores which are constantly 3-septate, measure  $17.5-21 \times 7.5-9\mu$  and are very tardy in the formation of their vertical septa.

#### THE VULGARIS SERIES

The name "vulgaris" series is used here merely for convenience for several species which seem to be derived from what is interpreted as *P. vulgaris*.

Table 1 represents, entirely aside from the application of any binomials, a series of collections from Wyoming in which there is a common basic spore form. This table (and those following) gives the characters of each collection by host and number. The figures for spore and ascus size and for spore septation are taken from one or more mounts, including anywhere from several to a dozen or more perithecia. They do not show any distribution curve, but are fairly accurate as to the range in size for each collection. Under perithecia, the figures represent the diameter, "D" stands for depressed-globbose, "C" for collapsing-pezizoid, "T" for basal tomentum, "S" for apical setae, and "G" for globose perithecia. Small letters indicate a lesser degree of the same condition.

The basic spore type in this series is fusoid-ellipsoid in form, slightly curved or inaequilateral and more acute than in the following "herbarum" series. This spore is at first 1- then 3-septate. A vertical wall is then laid down in the two central cells of this 4-celled spore. Following this, cross-walls are independently formed on the two sides of the vertical septum, so that they may occur on only one side of the vertical wall, or at different levels on the opposite sides. The end cells remain without a vertical septum.

If one glances at Table 1, it will be seen that the spore ranges of individual collections present an almost continuous overlapping series with gradually increasing size. The collections in section "A" have spores (fig. 3) of this basic type with 3-5 cross walls and measuring  $17-26 \times 7-10\mu$ , and are considered under the name of *P. vulgaris*. Section C of the table is a continuation of this same series, in which the spores (fig. 5) run larger,  $26-40 \times 9-15\mu$ , and are more constantly 5-septate. These appear to fit *P. rictophensis*. This increase in the number of cross septa is carried still further in the 7-septate species, *P. tomentosa*, *P. pleosphaerioides* and *P. punctata*.

In section B, of Table 1, we have a series of collections with spore sizes more or less parallel to those in section A, but which show the transition in spore form (fig. 4) from that of the *vulgaris* to that of the *herbarum* series. In these collections the spores are more constantly 5-septate and there is a tendency for a "Y"-shaped septum, or a transverse and vertical wall, to form in each end cell. This results in a 7-septate spore with vertically sep-

TABLE I

No.	Host	Spore Range	Septation	Asci	Perithecia
A					
1016a	Penstemon	17.5-21.5×7-9.5	3-5	75-120×14-18	3-350, D
1220	Bupleurum	18-23×7-8.5	3-5	70-88×14-18	250-350, d
1015	Castilleja	19.5-24×7.5-9	3-5	78-85×14-18	2-350, D, c, T
1056c	Aquilegia	19.5-26×7-9	3-7	70-80×16-18	250-300, D, C, t
1067a	Pedicularis	19.5-25×8.5-10.5	5	75-90×16-17	250-350, d, t
1185a	Draba	20-25×8.5-9.5	3-5	60-65×16-19	150-200, D, c, t
B					
1108a	Rudbeckia	19.5-26×9-10.5	5-7	78-100×19.5-23	2-300, t
1201	Penstemon	20-26×8-10.5	5-7	78-90×14-18	250-350, D, T
1159	Castilleja	21.5-24.5×8.5-9	5-7	78-88×17-19	2-300, D, C, t
1089	Penstemon	21.5-26×10-11	5-7	65-70×17-21	1-200, d, t
1086	Penstemon	21.5-28.5×9-12.5	5-7	85-96×21-22	2-250, t
1121a	Agastache	22-28×9-12	5-7	85-110×17-20	2-250, t
1078	Castilleja	22-27×9.5-11.5	3-7	70-78×16-18	150-200, d
1022	Umbellifer	23-28×9-12.5	7	110-135×18-22	2-400, d, t
1085	Solidago	23-28×10-12	5-7	75-88×19-21	2-250, d, t
C					
1168a	Senecio	26-32×9-11	5	78-90×20-22	250-450, C, T
1100b	Helianthella?	28-35×11-13	5	120-130×24-26	3-450, D, C, T
1127a	Achillaea	28.5-32×10-11	5	88-100×21-24	3-400, D, T
1113b	Erigeron	30-34×11-13.5	5	85-95×21-23	3-400, d, t
1121	Agastache	30-35×12.5-15	5	120-140×26-31	350, D, C, T
1119a	Osmorrhiza	30-35 (37)×11-14	5	78-110×20-22	350-400, D, C, T
1084	Umbellifer	30-39×12-13	5	100-120×23-27	2-350, D, C, T
1127	Achillaea	35-38×12.5-15	5	85-120×21-26	250-500, DT,
1280a	Senecio	35-40×12.5-14	5	134-175×27-32	3-400, d

tate end cells. Spores of these collections also tend to be broader and more rounded at the ends, although an inaequilateral form can be distinguished in many spores. These collections correspond to *P. Compositarum* and the continuation of these tendencies to form broader, larger, more oblong, more definitely 7-septate spores results in a complete intergrading series into forms like *P. herbarum*.

These collections are easily confused with *P. vulgaris*, and certain ones, such as Nos. 1159 & 1078 on *Castilleja* and 1056c on *Aquilegia*, show spores

of both types, and are difficult to place. The size of the perithecia and the amount of basal tomentum in both *P. vulgaris* and *P. Compositarum* is variable but shows no correlation with spore characters or host, as can be seen from Table 1. In the upper range of the *P. Compositarum* series, as in the series of *P. herbarum*, there is a tendency for some collections to form apical setae, which will be mentioned later.

In this situation, specific lines must be drawn in an entirely arbitrary fashion, for there will always be collections which will overlap such arbitrary limits.

#### PLEOSPORA VULGARIS Niessl

Pl. 1, Fig. 3

Perithecia causing scattered, black, conic, papillate pustules on the stem, globose or usually depressed-globose, becoming somewhat pezizoid collapsed with age, with more or less brown creeping tomentum at the base, but this usually beneath the epidermis and not visible superficially,  $100-350 \times 100-250\mu$ .

Ascii stout clavate with a thickened wall and a stout, short, claw-like base,  $70-120 \times 14-19\mu$ .

Spores biseriate, oblong- to fusoid-ellipsoid, ends usually acute but sometimes obtuse, often inaequilateral or slightly curved, 3-septate at first, then 5-septate, 2nd and 4th septa commonly incomplete, lacking or irregular, constricted at the central septum, with a vertical septum in each of the central cells but not in the end cells, rather dark brown,  $17.5-26 \times 7-10\mu$ .

Camp Davis: on *Penstemon glaber* Pursh, June 18 (1016a); *Bupleurum americanum* Coult. & Rose, July 4 (1220); *Castilleja flava* S. Wats., June 18 (1015); *Pedicularis groenlandica* Retz. (Willow Creek), June 28 (1067a), and *Senecio Rydbergii* A. Nels., June 19 (1033b).

Hoback Canyon: on *Aquilegia coerulea* James (Forest Camp), June 25 (1056c); *Draba luteola* Greene (Red Creek), June 29 (1185a).

Niessl (8, p. 187) says that *P. vulgaris* differs from *P. herbarum* only in the 5-septate, smaller spores and in the smaller ascii and perithecia. These American collections show spores which are more fusoid-ellipsoid and inaequilateral, but there is an intergrading series into *P. herbarum* as has been mentioned. Berlese (2, 2; 11) places *P. vulgaris*, *P. socialis* etc. as synonyms of *P. infectoria* Fck., and gives an excellent figure of the type of spore here discussed (Pl. 13, fig. 2), for this latter species. The spores of *P. infectoria* have been variously given as  $18-26 \times 9-12$  (Fuckel & Saccardo)  $17-26 \times 7-9$  (Winter),  $18-22 \times 8-10$  (Berlese) and  $15-21 \times 8-10$  (Ellis). An examination of a Fuckel collection (No. 463) in the Farlow Herbarium, which is apparently a syntype with Fung. Rhen. 2246, shows small spores  $15-18$  (20)  $\times 6-7\mu$  in perithecia which are crowded in linear blackened spots on grasses, in which respects it differs from these western

collections, which are, therefore, kept separate under the binomial *P. vulgaris*. Only comparison with Niessl's type can determine whether it is identical with these western collections.

### PLEOSPORA COMPOSITARUM Earle

Pl. 1, Fig. 4

Perithecia scattered, appearing as blackened conic pustules, often with an abundant surface growth of brown torulose hyphae, globose to depressed-globose, ostiole minute papillate, becoming collapsed in age, with more or less radiating tomentum at the base beneath the epidermis and sometimes with a few apical spines, when young,  $100-350 \times 100-250\mu$ .

Asci stout clavate, thick-walled, with a claw-like base,  $65-135 \times 14-23\mu$ .

Spores biseriate, oblong-ellipsoid, ends rounded, obtuse or with the lower half inaequilateral and more acutely tapered, 5- to 7-septate, with usually one vertical septum in each cell, including the end cells, in most cases,  $19.5-28 \times 8-12.5\mu$ , dark in color.

Camp Davis: on *Castilleja linariaefolia* Benth., July 3 (1078); *Penstemon glaber* Pursh., Aug. 3 (1201).

Junction of Hoback & Snake Rivers: on *Castilleja linariaefolia*, Benth., July 15 (1159).

Cream Puff Mt.: July 5, on *Penstemon Rydbergii* A. Nels. (1089); *P. stenosepalus* (Gray) Howell (1086) and *Solidago* sp. (1085).

Teton Pass Road: on Umbellifer, June 2 (1022); and South of Teton Pass: July 11, on *Rudbeckia occidentalis* Nutt. (1108a) and *Agastache urticifolia* (Benth.) Rydb. (1121a).

The species complex represented by the group of collections in section B of Table 1 is no doubt represented by a number of described species. *P. lepidiicola* Earle, *P. Senecionis* Earle, and *P. Compositarum* Earle are all of this series (with spores  $18-26 \times 7-10\mu$ ). Inasmuch as *P. Compositarum* is the first name (in page position) to be definitely fixed with this series, it is used here. This series probably also corresponds to the *P. media* of Niessl (8, p. 188), who says that that species differs from *P. vulgaris* chiefly in the darker spores and the vertical septum which extends through the end cells. He gives the spores as 5-septate, however, and  $18-23 \times 10-11\mu$ , which would correspond only to the smaller spored representatives of this series. Berlese (2, 2; 12) gives the spores of Niessl's material as  $22-24 \times 9-12\mu$ , and those of his var. *Limonum* as  $25-38 \times 10-12\mu$ .

The perithecia of this group often form a crown of setae on their upper surface. When the epidermis is persistent, these setae may have difficulty in penetrating it, or they may be deciduous in age, so that there is a great deal of variation in this character. In collections in the higher spore range and more constantly seven-septate, these setae are often persistent and have been described in Pyrenophora. *Pyrenophora Castillejae* Earle, and

*P. Clematidis* Earle are of this type. This type of spore, again, grades off gradually into that characteristic of *P. herbarum*. The spores of No. 1098, on *Solidago*, are definitely larger than those of No. 1108a, on *Rudbeckia*, but all intermediate variations are encountered. Host distribution again is not correlated with spore size.

### PLEOSPORA RICHTOPHENSISS E. & E.

Pl. 1, Fig. 5

Perithecia widely or thickly scattered, at first immersed, appearing under the epidermis as hemispheric black pustules, later free, superficial, depressed spheric, with a minute papillate ostiole, finally somewhat collapsed and with a more or less well developed radiate basal tomentum beneath the epidermis, but not visible superficially,  $250-500\mu$  in diameter.

Asci stout clavate with thickened walls and a claw-like base,  $80-108 \times 19-23\mu$ .

Spores biseriate in the ascus, fusoid-ellipsoid, inaequilateral or slightly curved, 5-septate, constricted at the central septum, with one vertical septum in the four central cells, end cells elongate and without a vertical septum,  $(26) 28-35 (40) \times (9) 11-14\mu$ .

Cream Puff Mt.: on umbellifer, July 5 (1084).

South of Teton Pass: July 11, on *Achillea Millefolium* L. (1127, 1127a); *Agastache urticifolia* (Benth.) Rydb. (1121); *Erigeron salsuginosus* Gray (1113b); *Glycosma* (*Osmorrhiza*) *occidentalis* Nutt. (1119a).

Togwotee Pass: July 8, on Composite (Helianthella?) (1100b)

Skyline Trail: on *Senecio crassulus* Gray, July 24 (1168a); and *Senecio* sp. (Overlook), Aug. 5 (1208a).

This species seems to be more alpine in its distribution than the two preceding. All of the collections were made above 9000 ft. elevation.

Ellis' N.A.F. 3523, of *P. richtophensis*, collected by Baker in Colorado, is identical with this group of collections, the spores  $(26-32 \times 10.5-12.5\mu)$  being in the lower portion of their range. This species has the spore form of *P. vulgaris*, but the spores are larger and more constantly 5-septate. The perithecia run somewhat larger and the asci somewhat broader than in that species.

The collection on *Achillea* of this species shows a mixture of perithecia of two types (1127 & 1127a), one containing spores  $28.5-32 \times 10-11\mu$  and the other, spores  $35-38 \times 12.5-16\mu$ . The spores were all 5-septate, but the two types were distinct enough to be easily picked out by the eye. Of some twelve perithecia examined, all but one contained only spores of one type or the other. The one exception had spores of the smaller type, with some spores running to  $35 \times 12.5\mu$ . Similar situations have been noted in other species and they are of special interest, for they suggest that there may be strains within these larger complexes, as to spore size, which may be more

constant within themselves, but that there may be some mechanism of hybridization which results in the overlapping variations usually found.

The following three species are all similar in having a 7-septate type of spore which could easily be derived from that of *P. rictophensis* by the insertion of an extra septum in each end cell.

### **Pleospora (Pyrenophora) tomentosa** sp. nov.

Pl. 1, Fig. 9

Perithecia scattered,  $300-400 \times 150-200\mu$ , depressed spheric, with a minute papillate ostiole, collapsing with age, remaining long immersed beneath the epidermis, with an abundant radiate growth of basal brown hyphae and some stiff setose hairs on the upper surface of the wall, which may project beyond the epidermis as brown setae.

Asci clavate, thick-walled, with a claw-like base,  $85-108 \times 19-23\mu$ .

Spores biseriate, fusoid-ellipsoid, slightly curved, muriform, 7-septate, constricted at the central septum, end cells without any vertical septum, yellow-brown,  $26-35 \times 10.5-13\mu$ .

Hoback-Snake River Junction, on *Castilleja linariaefolia* Benth., July 15 (1159a); and Teton Pass Rd., on *Rudbeckia occidentalis* Nutt., July 11, legit L. E. Wehmeyer (1108) (Type).

Perithecia dispersa, depresso globosa,  $300-400\mu$  diametro,  $150-200\mu$  alta, sub epidermate immersa, basi tomento brunneo, copioso, radiato, et in superiori parte paucis setis interdum supra epidermatem prolongatis praedita. Asci clavati, crasse membranosi,  $85-108\mu$  longi,  $19-23\mu$  lati, basi unguiculiformes. Sporae biseriatae, fusiformiter ellipsoidales, paululo curvatae, muriformes, 7-septatae, ad septum medium constrictae, lutei-brunneae,  $26-35\mu$  longae,  $10.5-13\mu$  crassae, cellulis terminalibus non verticaliter septatis.

Specimen typicum in caulibus vetustis *Rudbeckiae occidentalis* Nutt., prope Teton Pass, Jackson, Wyoming, 11 Jul., 1940, legit L. E. Wehmeyer, sub numero 1108.

It is quite possible that this and the following species are growth forms or varieties of the same species. If so, it illustrates the difficulty of separating *Pleospora* and *Pyrenophora*. On *Castilleja*, the overlying stem tissues are quite adherent and only a very few of the setose hairs, which are borne in addition to the basal tomentum, penetrate these tissues. On *Rudbeckia*, these overlying tissues are more easily ruptured, the setiform hyphae are more abundant, and the *Pyrenophora* character is quite evident.

In the following species, the epidermis is thin and very soon ruptured. As a result, the perithecia are very soon erumpent-superficial, become globose, instead of flattened globose, and are densely covered over the entire wall by setiform hyphae, giving them the appearance of a *Pleosphaeria*. The large globose perithecia may also be responsible for the more elongate cylindric ascii and uniseriate spores, characteristic of this species, for the ascii are obviously crowded in the flattened perithecia of *P. tomentosa*.

The spores of *P. tomentosa* and *P. Compositarum* are easily confused.

The figs. 4 & 9 of Plate 1 show that on *Castilleja* they are somewhat intermediate. The material seen of this species was sparse and was mixed with *P. Compositarum* on *Rudbeckia*. Further collections are needed for confirmation.

**Pleospora (Pyrenophora) pleosphaerioides** sp. nov.

Pl. 1, Figs. 6-7

Perithecia thickly scattered or crowded, arising beneath the epidermis but soon erumpent and almost entirely superficial, large, globose, 400-600 $\mu$  in diameter, tomentose at the base with creeping brown hyphae and covered over the entire wall surface, particularly about the ostiole, with dark brown, tapered, blunt, non-septate, upright setae, 50-150 $\times$ 4-5 $\mu$ . Ostiole small and widely punctate.

Asci long cylindric, thick-walled, with a claw-like base, 160-200 $\times$ 17-19 $\mu$ .

Spores overlapping uniseriate, fusoid-ellipsoid, somewhat curved, muriform, 7-septate, with the end cells, and often some central cells, lacking vertical septa, constricted at the central septum, yellow-brown, 32-39 $\times$ 9.5-12.5 $\mu$ . These spores may become 9-septate by the insertion of faint or irregular secondary septa.

South of Teton Pass: on *Gilia Watsonii* Gray, July 11, legit L. E. Wehmeyer (1118a) (Type).

Perithecia dense dispersa, sub epidermate orientia, deinde superficialiter erumpentia, globosa, 400-600 $\mu$  diametro, basi tomentosa, hyphis tomenti radiatis, procumbentibus, brunneis; pariete totaliter investo praecipue circum ostiolum cum setis atrobrunneis, sursum angustatis, obtusis, nonseptatis, erectis, 50-150 $\mu$  longis, 4-5 $\mu$  crassis. Ostiolum parvum late apertum. Asci longe cylindrici, crasse membranosi, basi unguiculiformes, 160-200 $\mu$  longi, 17-19 $\mu$  crassi. Sporae imbricatae, uniseriatae, fusiformiter ellipsoideae, paulum curvatae, muriformes, 7-septatae, luteibrunnae, 32-39 $\mu$  longae, 9.5-12.5 crassae, cellulis terminalibus et saepe interioribus absque septis verticibus.

Specimen typicum in caulibus vetustis *Giliae Watsoni* Gray, prope Tetón Pass, Jackson, Wyoming, 11 Jul., 1940, legit L. E. Wehmeyer, sub numero 1118a.

This species has spores similar to but larger than those of *P. tomentosa*, but the perithecia are large, globose, becoming superficial and densely covered with upright setae, so that they resemble a *Pleosphaeria* at maturity. The asci are long cylindric and the spores uniseriate also. These characters seem correlated with the free superficial growth of the perithecia (see last species).

**Pleospora punctata** sp. nov.

Pl. 1, Fig. 8

Perithecia thickly scattered as minute dots, the barely erumpent ostioles, forming rather sharply limited grayish colored areas on the stem, small, globose, thin-walled, 120-150 $\mu$  in diameter.

Asci saccate, thick-walled, with a claw-like base, 75-85 $\times$ 21-25 $\mu$ .

Spores biseriate, fusoid-ellipsoid, inaequilateral or slightly curved, 5- to 7-septate, constricted at the central septum, upper half commonly more broadly rounded, lower half more acutely tapered, with one vertical septum in each central cell, but not in the end cells,  $26-30 (33) \times 9-11 \mu$ .

Elk Refuge, Jackson, Wyo.: on *Scirpus validus* Vahl, July 1, legit L. E. Wehmeyer (1071) (Type).

Perithecia dense dispersa (sicut macula minuta) areas griseas valde circumscripas in caulis *Scirpi validi* occupantia, globosa,  $120-150 \mu$  diametro; pariete tenui; ostiolo perminuto vix erumpente; ascis sacciformibus,  $75-85 \mu$  longis,  $21-25 \mu$  latis, crasse membranosis, basi unguiformibus; sporis biseriatis,  $26-30 (33) \mu$  longis,  $9-11 \mu$  crassis, fusiformiter ellipsoideis, paulum curvatis vel inaequilateralibus, 5-7-septatis, ad septum medium constrictis, plerumque in parte superiore latiuscule rontundatis, in parte inferiore acutiuscule angustatis; cellulis interioribus verticaliter uniseptatis, eis terminalibus nonseptatis.

Specimen typicum in caulis vetustis *Scirpi validi* Vahl, prope Elk Refuge, Jackson, Wyoming, 1 Jul., 1940, legit L. E. Wehmeyer, sub numero 1071.

This species, again, has 7-septate fusoid spores similar to the last two species, but the perithecia are minute, smooth and entirely immersed in the stem. The spores are similar to those of *P. juncicola*, except that the latter are described as flattened, clathrate. *P. punctiformis* and *P. spinosella* are also similar species but they both have smaller spores ( $20-24 \mu$  long) and those of the former species are clathrate according to Berlese (2, 2; 32).

#### THE "HERBARUM" SERIES

The "herbarum" series consists of another large group of collections with a basic spore form, arising from the previous type and characteristic of the *Pleospora herbarum* complex. It has already been pointed out that there is a continuous series of intergrading forms from those typical of *P. vulgaris* through *P. Compositarum* to those typical of *P. herbarum*. The basic spore of this group has seven transverse septa, with the end cells vertically septate, and is oblong-ellipsoid with rounded ends rather than fusoid-ellipsoid with acute ends as in the preceding series. This spore type is also usually asymmetrical; the portion above the median constriction is usually broader, shorter and more rounded, whereas the portion below this constriction, is longer, narrower, and in some cases tapered or inaequilateral.

In Table 2, the western collections of this type with seven-septate (3-1-3) spores are arranged according to spore size. Here again the specific separation must be largely arbitrary, as represented by the solid lines. In the section A are the collections which fall in the spore range of *Pleospora herbarum* as interpreted by Rabenhorst. The tendency to form stiff hairs about the ostiole, which may penetrate through the epidermis, which was seen in the larger spored forms of the previous series, is continued into this group and the two collections in section B, placed under *Pleospora (Pyrenophora) Tetraneuridis*, are of this sort. Section C, includes a group of collections in which the spore size overlaps that of section A, but the

halves of the spore are more symmetrical, usually broader, and the spores reach a much greater size than in *P. herbarum*. This group has been described as *P. Balsamorrhizae*.

The group of collections presented in Table 3 is the most confusing of these western Pleosporas. They include all those collections of this spore type with more than seven septa and represent the tendency to lay down extra cross walls. These extra transverse septa first occur in the lower half of the spore giving 8-9- or 10-septate spores with a 3-1-4, 3-1-5 or 3-1-6 arrangement of the septa. In the large spored forms extra septa may also

TABLE 2

No.	Host	Spore Range	Septa-tion	Asci	Perithecia
A					
1201C	Penstemon	26-35×12.5-16	7	80-96×18-26	2-400
1055	Sphaeralcea	25-34×11-16	7	88-97×23-26	250-350, D, C
1110a	Lupinus	26-33×10.5-12.5	7	98-110×26-38	3-350, d, c
1121d	Agastache	27-35×12-14.5	7	110-145×24-36	3-400, T
1033a	Senecio	28-34×12.5-16	7	100-145×26-32	150-300, D, C
1170	Horkelia	32-35×14-16	7	105-125×33-35	200, D
B					
1096a	Pedicularis	28-35×10.5-12.5	7	90-120×20-26	1-200, G, S
1176	Zygadenus	32-37×10.5-14.5	7	100-115×23	250-350, G, S
C					
1221	Pseudocymopteris	33-42×14-18	7	105-160×35	1-200, D
1143	Polemonium	33-42.5×14-19.5	7	115-125×35	2-300, d, t
1063	Balsamorrhiza	42-63×19.5-25	7	133-175×53-65	150-250, t

occur in the upper portion of the spore, which is more persistently 3-septate than the lower half.

This increase in the number of septa is correlated somewhat, but not completely, with the increase in size of the spore. Ascus measurements are also correlated in a general way with the size of the spore. The perithecia are extremely variable as to size, amount of tomentum and the presence or absence of setae, which seem to be correlated in no way with spore form or host. A comparative study of these collections indicates that the septation of the spore, although variable, is much more dependable than any other character. Here again, therefore, the specific demarcation is made arbitrarily as indicated by the solid lines.

In section A, the spore size overlaps that of *P. herbarum*, but always runs higher. Likewise, the spores are fundamentally 7-septate, but there are always some spores showing an extra septum in the lower half. In section B, the spore sizes again overlap, somewhat, those of section A,

but the fundamental number of septa is 9, with a 3-1-5 arrangement, and commonly with an extra septum, in either half. In section C, the spore size is about the same as in section B, but the spores are fundamentally 11-septate, with a 3-1-6 or a 3-1-7 arrangement. The one collection in section D has larger spores with a still greater number of septa.

There is no doubt that a large number of species could, and have been erected upon minor characters within this "herbarum" group. As a matter of fact, thirty-nine varieties of *P. herbarum* alone have been erected, covering a range of variation wider than that covered by both Tables 2 and 3. It is the writer's belief, however, that such indiscriminate erection of species with no correlation with those already erected, is the direct cause of much confusion. What is needed is a preliminary conservative separation of species upon the basis of the natural variation. When the background of such a conservative natural arrangement is known, it will be much easier to recognize minor variations from this pattern, and segregate them accordingly.

#### PLEOSPORA OLIGASCA Bub.

Pl. 1, Figs. 10-11

Perithecia thickly scattered, minute,  $70-150\mu$  in diameter, conic-globose, with a comparatively large conic, often curved, beak-like ostiole, soon erumpent superficial.

Asci few (1-5), at first broad saccate, almost globose, with a thickened apical wall and a claw-like base, becoming broad clavate,  $45-70 \times 30-60\mu$ .

Spores 2- to 3-seriate, oblong-ellipsoid, brown, 4- to 6-septate, constricted at the second or third septum, upper half short, stout, globose and 1- to 2-septate, lower half longer, narrower, oblong, and 2- to 3-septate, with one, or rarely two vertical septa in all cells except the end cells in some cases, extremely variable in size with age,  $23-35\mu$  long,  $10.5-14\mu$  in diameter in the upper and  $8-11\mu$  in the lower half.

Camp Davis: on *Sieversia ciliata* (Pursh) G. Don, June 17 (1017).

This is a very distinctive little species with minute sclerotial perithecia (fig. 10) of the Scleroplea type, large ostioles, few saccate ascii and 4- to 6-septate spores (fig. 11) which do not fit directly into this herbarum series and may represent a separate series.

This collection (no. 1017) fits perfectly the description of *P. oligasca*, although the spore measurements given for that species are at the lower end of this spore range. The spores seem to increase in size after being formed in the ascus, which swells to a clavate form when released from the small perithecia. Clements Crypt. Form. Colo. No. 34, under the unpublished name of *Pleospora cybospora*, is also this species, on *Drymocallis fissa*, from Colorado. Bubak reports his collection from an elevation of 2000 meters.

**Pleospora herbarum** (Pers.) Rab. var. **occidentalis** var. nov.

Pl. 2, Fig. 13

Perithecia scattered, often mixed with other species of Pleospora or other fungi, depressed-spheric, with a minute central papillate ostiole,  $250-400 \times 150-300\mu$ , collapsing somewhat with age, sometimes with a few basal hairs, but not obviously tomentose, immersed beneath the epidermis, which is eventually exfoliated.

Asci clavate, thick-walled, with a claw-like base, elongating at maturity,  $80-145 \times 20-28 (35)\mu$ .

Spores biseriate to obliquely uniserial upon ejection, oblong-ellipsoid, often inaequilateral, particularly in the lower half, which may be tapered, slightly bent, or curved, 7-septate, rather dark brown, with 1-2 vertical septa in each cell,  $26-35 \times 11-16\mu$ .

Hoback Canyon: on *Sphaeralcea rivularis* (Dougl.) Torr. (Forest Camp), June 25, legit L. E. Wehmeyer (1055) (Type).

Camp Davis: on *Senecio Rydbergii* A. Nels., June 9 (1033a); and *Penstemon glaber* Pursh, Aug. 3 (1201c).

South of Teton Pass: July 11, on *Agastache urticifolia* (Benth.) Rydb. (1121d); and *Lupinus parviflorus* Nutt. (1110a).

Skyline Trail: on *Horkelia (Ivesia) Gordonii* Hook., July 24 (1170).

Perithecia dispersa, depresso globosa, ostiolo minuto papilliforme praedita,  $250-400\mu$  laterali-ter diametentia, altitudine  $150-300\mu$ , aetate collapsa, interdum basi pilis paucis investa, sub epidermate immersa. Asci clavatae, maturitate  $80-145\mu$  longi,  $20-28 (35)\mu$  crassi; basi unguiculiformes; pariete crasso. Sporae biseriatae vel oblique uniserialatae, oblongi-ellipsoidales, media parte paulum constrictae, saepe inaequilaterales (principue in parte inferiore aut augustata aut curvata), 7-septatae, modice atribrunneae,  $26-35\mu$  longae,  $11-16\mu$  crassae; cellulis septis 1 vel 2 verticalibus praeditis.

Specimen typicum in caulinis vetustis *Sphaeralceae rivulari* (Dougl.) Torr. ad Forest Camp, Hoback Canyon, Jackson, Wyoming, 25 Jun., 1940, legit L. E. Wehmeyer, sub numero 1055.

A forma typica Europaea differt sporis atrioribus saepe deorsum asymmetricis et aliquantum latioribus.

The binomial *Pleospora herbarum* is applied to a species complex (including some 39 varieties) into which all sorts of 7-septate entities have been dumped. The *Sphaeria herbarum*, of both Persoon and Fries, were probably mixed species, and without an examination of their original material, or microscopical data (lacking from their descriptions) it is impossible to place their interpretations of this name. It seems best to the writer to base *P. herbarum* on the excellent series of exsiccatai (Rab. Herb. Myc. 547a-e) of this species on various hosts, and this has apparently been done by most authors.

The Wyoming collections differ in certain respects from these European exsiccatai, and these differences are recognized by the erection of a new variety, *occidentalis*, which is distinguished by the somewhat darker colored, more inaequilateral spores (fig. 13) which are more consistently

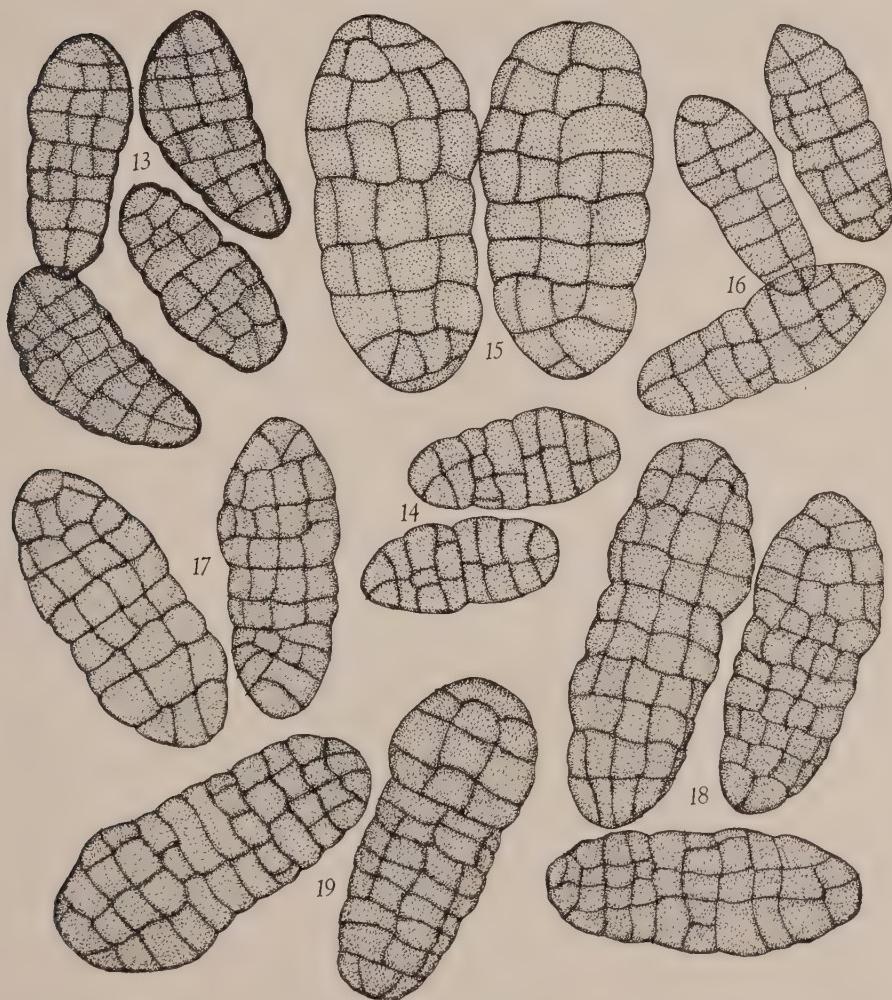


PLATE 2. 13. *Pleospora herbarum* var. *occidentalis* var. nov. showing characteristic asymmetry in two spores. 14. European *Pleospora herbarum* (Pers.) Rab., (from Rab., Herb. Myc. 547). 15. *Pleospora Balsamorhizae* Tracy & Earle. 16. *Pleospora (Pyrenophora) Tetraneuridis* Earle. 17. *Pleospora stenospora* Schroet. 18. *Pleospora njegusensis* Bub. 19. *Pleospora montana* sp. nov. Scale, 1 mm. = 1  $\mu$ . Figs. 13-19. Ascospores.

biseriate in somewhat shorter broader asci. The spores of the European species (Pl. 2, fig. 14) are light yellow brown with the lower portion straight but somewhat narrower. In these western collections, the spores are a darker reddish-brown and the lower portion is often tapered, slightly curved or inaequilateral. In Rabenhorst's exsiccati the asci are  $160-215 \times 21-26\mu$ , whereas in this variety they are  $80-145 \times 20-28 (35)\mu$ . The separation of this species and variety from the large spored forms of *P. Compositarum* is purely arbitrary. On the other hand, it grades off into the next species which differs only in the more symmetrical spores, generally smaller perithecia, and greater range in spore size.

#### PLEOSPORA BALSAMORRHIZAE Tracy & Earle

Pl. 2, Fig. 15

Perithecia small,  $100-250\mu$  in diameter, thickly scattered beneath the epidermis, globose at first, finally somewhat flattened but not collapsing, with a minute papillate ostiole and a few coarse radiating basal hyphae, which are not apparent except under a microscope.

Asci saccate, then broad clavate, thick-walled, with a claw-like base,  $115-175 \times 35-65\mu$ .

Spores 2- to 3-seriate, oblong-ellipsoid, straight, ends blunt, broad, constricted at the central septum, 7-septate (rarely 8-septate in large old spores), yellow brown at first becoming black brown to opaque, halves symmetrical, variable in size,  $33-63 \times 14-25\mu$ .

Hoback Canyon: June 16, on *Pseudocymopterus anisatus* (Gray) C. & R. (1221); and *Polemonium viscosum* Nutt. (1143).

Camp Davis: on *Balsamorrhiza sagittata* (Pursh) Nutt., June 16 (1063).

This species is characterised by the small perithecia and the large, broad, 7-septate spores (fig. 15). *P. Balsamorrhizae* is difficult to interpret because of its apparent extreme variation in spore characters. The type (Baker, Earle, and Tracy, Plants S. Colo. No. 1097) shows spores which are broad ellipsoid, pale yellow brown, 7-septate and  $30-55 \times 16-21\mu$ . An unpublished variety, "perseptis," is distributed in Clements Crypt. Form. Colo. No. 439, which has spores which are darker brown, almost opaque, more elongate fusoid, often showing 4 or even 5 septa in the lower half, and  $50-60 \times 21-26\mu$ . At first these appear to be quite distinct, but intermediate conditions occur on this last exsiccatus, and in No. 1063, on *Balsamorrhiza*, both types of spores are found intermingled on the same stem and in identical appearing perithecia. The typical, young, pale spores of the type differ from *P. herbarum* only in being larger, particularly broader, and with the lower half practically as broad as the upper. The larger, darker, 8- to 9-septate spores, on the contrary, are very much like those of *P. njegusensis*, but become even larger than in that species. In fact No. 1025a, of *P. njegusensis*, on *Balsamorrhiza*, may be this species. In this

last collection, however, the smaller spores, as well as the larger, have 4-5 septa in the lower half. The two collections on *Pseudocymopteris* and *Polemonium* do not show these larger, more septate spores, and appear more as examples of a large spored *P. herbarum*. This situation, again illustrates the difficulty of drawing sharp specific lines.

## PLEOSPORA (PYRENOPHORA) TETRANEURIDIS Earle

Pl. 2, Fig. 16

Perithecia loosely scattered, 100-350 $\mu$  in diameter, pyriform to globose at first, then depressed or even collapsing, formed beneath the epidermis

TABLE 3

No.	Host	Spore Range	Septation	Asci	Perithecia
A					
1175	Rydbergia	35-41 $\times$ 14-17	(7)8	95-140 $\times$ 35-39	2-300, T
1117	Senecio	35-42 $\times$ (13) 18-19	7(8)	115-170 $\times$ 32-38	250-350, D, C, T
1167	Linum	37-44 (48) $\times$ 14-19	7(8-9)	110-140 $\times$ 38-42	2-250, d, t
1173a	Hedysarum	37-42 $\times$ 16-18	(7)8	90-133 $\times$ 30-35	3-400, T, S
B					
1025a	Balsamorrhiza	33-44 $\times$ (13) 16-19	8(9)	115-160 $\times$ 44-50	250-350, D, c
1176a	Zygadenus	34-44 $\times$ (13) 14-17	9	105-125 $\times$ 32-35	2-300, d, t
1128	Valeriana	37-47 $\times$ 14-18	9(10)	115-150 $\times$ 39-42	
1063a	Balamorrhiza	39-50(60) $\times$ 14-18	(8)9	175-210 $\times$ 30-40	250-300, S
1110	Lupinus	39-51 $\times$ 16-19.5	9(10-11)	135-145 $\times$ 40-45	150-250, d, T
1134c	Linum	41-46 $\times$ 16-20	9(10)		450, T
1211	Gilia	31-54 $\times$ (17) 21-23	9(10-11)	150-180 $\times$ 40-55	250-400, D
1121e	Agastache	42-48 $\times$ 16-18	9(10)	125-150 $\times$ 40-45	3-400
1124a	Clematis	42-50 $\times$ 16-19	9(10)	105-135 $\times$ 43-47	250
1096	Pedicularis	43-50 $\times$ 18-25	9(10-11)	160-220 $\times$ 43-45	D, T, S
1118	Gilia	43-48 $\times$ 20-25	9(10-11)	160-175 $\times$ 50-53	
1126d	Hedysarum	44-53 $\times$ 15-19	9(10-11)	140-150 $\times$ 47-52	2-300, G, t
1173c	Hedysarum	46-53 $\times$ 17-18	9(10)	175-180 $\times$ 30-35	3-400, T, S
C					
1101	Lupinus	41-51 $\times$ 16-21.5	11(10)	125-142 $\times$ 50-55	150-300, G, T
1103	Lupinus	41-53 $\times$ 17.5-21	11(12)	175-210 $\times$ 57-60	3-350, G, T
1107	Lupinus	43-57 $\times$ 17-21	11(10-12)	125-135 $\times$ 40-45	2-300, G, T
D					
1134h	Linum	68-80 $\times$ 23-28	11(14)		

which falls off. Perithecia thin-walled, membranous, covered above with upright, stiff, setose, tapered, brown, hairs, up to 300 $\mu$  in length and 4-6 $\mu$  in diameter, which are sparingly septate.

Asci clavate, thick-walled, with a claw-like base, 90-115 $\times$ 23-26 $\mu$ .

Spores biseriate, fusoid- to oblong-ellipsoid, with ends either rounded or

acute, mostly straight, 7-septate, constricted at the central septum, with 1 or 2 vertical septa in each cell, one end often narrower than the other,  $28-37 \times 10.5-14.5\mu$ .

Togwotee Pass: on *Pedicularis Hallii* Rydb., July 8 (1096a).

Skyline Trail: on *Zygadenus alpina* Blank., June 24 (1176).

The spores of this species might be confused with either *P. tomentosa* or *P. herbarum*. They differ from the former in having septate end cells and usually more than one vertical septum. The latter species has perithecia which are not setose. *P. Tetraneuridis* represents the tendency of some members of this herbarum series to produce setose perithecia and is its Pyrenophora representative. This seems to be a characteristic of alpine forms, and suggests a close relationship to *Pyrenophora chrysospora* Niessl of Europe and to such similar species as *P. oligotricha* (Niessl) B. & V., *P. Tragacanthae* Berl. etc. *Pyrenophora Castillejae* and *P. Clematidis* of Earle have similar, but smaller spores of the *P. Compositarum* type and show very few setae, if any, in their type material. *P. Eriogoni* Earle has somewhat larger spores, but very few setae and his *P. Tetraneuridis*, which is on leaves, shows definitely spiny perithecia, particularly when young. The spores in the type of *P. Tetraneuridis* (N.Y.B.G., Earle Herb. No. 1068) are  $30-37 \times 12-18\mu$ . Whether these all represent separate species, and where the specific lines can be drawn or whether they should all be placed in the same species complex, can only be decided by the study of a much larger series of collections than were available to the writer. Both of the Wyoming collections were obtained at about 10,000 ft. elevation.

#### PLEOSPORA STENOSPORA Schroet.

Pl. 2, Fig. 17

Perithecia rather widely scattered, immersed, or rarely erumpent-superficial,  $250-450\mu$  in diameter, globose or slightly depressed, only rarely collapsing, walls rather thick, of coarse black parenchyma, usually with more or less basal tomentum and occasionally with a few spine-like setae projecting through the epidermis.

Ascii clavate, thick-walled, with a claw-like base,  $90-170 \times 30-42\mu$ .

Spores biseriate, oblong-ellipsoid,  $33-44(48) \times 17-19\mu$ , with several vertical septa in each cell, constricted at the central septum, somewhat above the middle; upper half usually shorter and broader with blunt rounded apex and three septa; lower half longer, narrower, often with a tapered, more acute end and commonly with an irregular angular arrangement at the lower end of 3 or 4 transverse or oblique septa.

Skyline Trail: July 24, on *Hedysarum* sp. (1173a); *Linum Lewisii* Pursh (1167); *Senecio* sp. (1177); and *Rydbergia grandiflora* (Pursh) Greene (1175).

It is interesting to note that although these collections were segregated

entirely on morphological grounds, they all came from the same locality, but on different hosts, at an elevation of about 10,000 feet. This species is very similar to the European *P. herbarum* except that the spores are slightly larger and tend to be 8-septate, because of the irregular septation in the lower end of the spore. On *Hedysarum* and *Senecio* the perithecia may produce a few stiff hairs which may penetrate the epidermis. On *Senecio* the perithecia are pezizoid collapsed and on *Hedysarum* they are globose. The constancy of such minor variations cannot, however, be judged from so few collections.

There are a score or more species described with 7-septate spores within this size range, but only a few of these vary to the 8- or 9-septate condition. Of these, *P. Van Hoffenii* Henn. has somewhat smaller and *P. Ephedrae* Fabre somewhat larger perithecia (both have 7- to 9-septate spores,  $35-45 \times 11-14\mu$ ). *P. laxa* Ell. & Galw. is also similar but has smaller perithecia and somewhat different spores. *Pleospora (Pyrenopora) Robertiana* Boy. & Jacz., with spores  $35 \times 14\mu$  might fit those collections with setose perithecia. *P. bobanensis* Bub. has somewhat larger spores ( $42-48 \times 15-19\mu$ ). *P. stenospora* Schroet., on *Anemone*, from Labrador, with spores  $33-38 \times 11-14\mu$  and 8-septate, seems to fit this group best, and the name, therefore, is here used provisionally.

#### PLEOSPORA NJEGUSENSIS Bub. ?

Pl. 2, Fig. 18

Perithecia scattered to thickly scattered over wide areas, formed beneath the epidermis, but often erumpent-superficial, varying from globose to somewhat depressed, smooth, with slight basal tomentum, or with basal tomentum and a few upright setae, often pezizoid or irregularly collapsed,  $200-400\mu$  in diameter.

Asci clavate, thick-walled, with a claw-like base,  $105-220 \times 32-55\mu$ .

Spores biseriate, oblong-ellipsoid, ( $33$ )  $37-54 \times 15-20$  ( $23\mu$ ), constricted at the fourth septum, unequally bipartite, upper half broader, shorter and 3-septate, lower half longer, narrower and somewhat tapered, mostly with 5 septa but sometimes with a 6th transverse septum inserted, and with several vertical septa. Rarely, there is a fourth septum in the upper half. This gives a 9- to 11-septate spore.

Camp Davis: on *Balsamorrhiza sagittata* (Pursh) Nutt. (1063a).

Glory Mt.: on *Balsamorrhiza sagittata* (Pursh) Nutt. (1025a).

South of Teton Pass: July 11, on *Gilia Watsonii* Gray (1118 & 1211); *Valeriana* sp. (1128); *Lupinus parviflorus* Nutt. (1110); *Linum Lewisii* Pursh (1134c); *Agastache urticifolia* (Benth.) Rydb. (1121e); *Clematis Douglasii* Hook. (1124a); *Hedysarum uintahense* A. Nels. (1126d).

Skyline Trail: July 24, on *Hedysarum* sp. (1173c); and *Zygadenus alpinus* Blank. (1176a).

Togwotee Pass: on *Pedicularis Hallii* Rydb., July 8 (1096).

This seems to be ubiquitous in the alpine area for all the collections, on many different hosts (except the one from Camp Davis), came from elevations of over 9000 ft. There is a good deal of variation in the spore size of these collections, but they all differ from the previous species in having at least five septa in the lower half of the spore. Occasionally there are 6 septa in the lower half, and rarely four septa in the upper half. Some collections such as 1063, on *Balsamorrhiza*, 1096, on *Pedicularis*, and 1110 on *Lupinus*, may show a few upright stiff hairs and approach the *Pyrenophora* type. Such minor differences, however, do not seem constant enough to justify specific separation.

Described species having this range of spore size and septation are *P. papillata* Karst., *P. Collaltina* Sacc. & Speg., *P. Prostii* Pass. & Roum., *P. Straminis* Sacc. & Speg., *P. ligni* Karschst. and *P. njegusensis* Bub. Berlese (2, 2; 26-27) disagrees with the original descriptions of all of the first four species, as to spore size and septation, on the basis of examination, apparently, of authentic material. *P. njegusensis*, with spores  $38-48 \times 15-19\mu$  and 8-10 septate seems to fit this group fairly well although the spores of the Wyoming collections are seldom 8-septate. This binomial is used with reservations, until comparison with more authentic material can be made.

### *Pleospora montana* sp. nov.

Pl. 2, Fig. 19

Perithecia rather small,  $150-300\mu$ , with a rather prominent conic ostiole, wall thick, composed of coarse, dark colored parenchyma, rather scattered at first, then erumpent-superficial, globose or only slightly depressed, smooth or with a basal tomentum or occasionally with a few upright, septate, brown setae, which are  $4-5\mu$  in diameter.

Asci comparatively few, saccate to broad clavate, thick-walled, with a claw-like base,  $125-210 \times 40-60\mu$ .

Spores 2- to 3-seriate, oblong-ellipsoid, muriform, constricted at the fourth septum, dark brown, 10-11- or rarely 12-septate; upper half shorter and broader, rounded and 3-septate; lower half longer and narrower, rounded, 6- or usually 7-septate;  $41-57 \times 16-21\mu$ . There is rarely a fourth septum inserted in the upper half. There are several vertical septa in each cell.

Togwotee Pass: July 8, on *Lupinus candidans* Rydb. (1101) (Type) & (1107); and *L. (parviflorus)* Nutt. (?) (1103).

Perithecia plus minusve dispersa, immersa, deinde superficialiter erumpentia, globosa vel paulum depressa,  $150-300\mu$  diametro, glabra vel basi tomentosa, vel interdum setis paucis, rectis,  $4-5\mu$  crassis praedita; ostiolo prominenti conico; pariete crasso ex parenchymate crasso fusco; ascis paucis,  $125-210\mu$  longis,  $40-60\mu$  latis, sacculiformibus vel late clavatis, crasse membranosis, basi unguiformibus; sporis  $41-57$  longis,  $16-21\mu$  crassis, 2- vel 3-seriatis, oblonge ellipsoideis, muriformibus, ad septum quartum constrictis, atribrunneis, 10- vel 11- (vel 12-) septatis, dimidio

superiore brevi latoque, rotundato et 3-septato, interdum 4-septato, dimidio inferiore longiore et angustiore etiamque rotundato, 6- vel plerumque 7-septato; cellulis omnibus verticaliter multisepatis.

Specimen typicum in caulis vetustis *Lupini candicans* Rydb., ad montem dictum Breccia Peak, prope Togwotee Pass, Teton Co., Wyoming, 8 Jul., 1940, legit L. E. Wehmeyer, sub numero 1101.

Another alpine species, with all collections found at the same locality and on the same host genus. It is characterised by rather dark brown spores with the septum arrangement of 3-1-6 or 3-1-7. The perithecia are more stoutly subglobose than in many other species. The only described species which approaches this is *P. megalotheca* Tracy & Earle with spores 40-45 $\times$ 16-20 and 11- to 13-septate. Type material (Pl. South Colo. No. 172) of this species yielded several species of Pleospora but none that would fit the original description.

#### PLEOSPORA AMPLISPORA E. & E.

Perithecia and ascii not seen. Spores oblong-ellipsoid, constricted above the middle, upper half shorter and broader, 4- to 5-septate, lower half longer and narrower, 7- to 8-septate, with 2 to 4 vertical septa in each cell, entire spore 12- to 14-septate, 68-80 $\times$ 23 $\mu$ .

South of Teton Pass: on *Linum Lewisii* Pursh, July 11 (1134h).

Only one crushed perithecium was seen of this species, but the spores are very large and characteristic, and show the extreme septation of the upper half of the spore. The two species, *P. gigantasca* Karst. and *P. amplispora* E. & E., which fit this collection are considered to be synonyms by Berlese (2, 2; 28) and were described in the same year (1884). Inasmuch as *P. amplispora* was described from the western United States, on Lupinus, that name is used here.

#### THE "CLATHRATE" SERIES

The species of Pleospora with a clathrate or flattened spore were placed in a separate genus Clathrospora, by Rabenhorst, which is a much more distinct separation than the one based on setose ostioles, in the genus Pyrenopspora. These clathrate species seem to be a common and characteristic component of the arctic-alpine fungous flora of many regions. All but one of the Wyoming collections with clathrate spores are similar in spore form with many intergrading variations. This common spore form is broadly rhomboid-ellipsoid to clavate-ellipsoid (see figs. 31-34) without sharp constrictions at the 3 to 5 septa and, in face view, showing a single central vertical septum in the central cells but not in the end cells. The number of septa seems to be quite constant (in any one collection), but the variations in spore size, again, gives an overlapping series.

In Table 4, the collections with 3-septate spores are arranged according to spore size. Ascus size is fairly constant and the perithecia are charac-

teristically flattened spheric, soon collapsing in a pezizoid manner and with a dense basal radiating tomentum (Pl. 3, fig. 30). The last two collections (section B) show spores and asci with rather definitely larger measurements and are placed in a separate species *P. diplospora*. The collections in

TABLE 4. *Spores clathrate, 3-septate*

No.	Host	Spore Range	Asci	Perithecia
A				
1032	Syntheris	21-31×10-12.5×7-9	75-95×21-24	2-300, D, C, T
1110c	Lupinus	23-26×10.5-11.5×8.5-10	88-98×19-21	2-250, D, t
1129a	Delphinium	23-28×12.5×8-9	85-90×21-25	3-500, D, C, T
1133b	Sambucus	23-30×12.5-13×9-10.5	85-95×21-22	2-400, D, C, T
1158	Stephanomeria	24.5-26×12.5×9-10	85-95×25-26	2-300, D, C
1134f	Linum	24-26.5×10.5-12.5×8-9		
1209	Brickellia	24-27×10.5×8-9	70×26	250-300, D, C, t
1124b	Clematis	24-28×10-12.5×7.5-9	78-95×19-23	350-400, D, C, T
1086a	Penstemon	24-27×11-12.5×9-10.5	88-96×20	D, C, T
1166a	Carum	25-26×10-12.5×8-9	88-100×20-21	300-350, D, C, T
1023b	Linaria	25-27×10.5-12.5×9-10	70×23	D, C, T
1128a	Valeriana	25-28.5×11-12.5×9-11	85-96×20-22	3-400, D, C, T
1025	Basamorrhiza	25-28.5×12.5×8.5-9.5	85-105×20-22	300, D, C, T
1208b	Senecio	25-29×11-12.5×8-9.5	78-97×23-26	
1126b	Hedysarum	26-28×12.5×9		
1130b	Lupinus	26-28×10-11×9		
1100a	Helianthella	26-29×12.5×7.5-9	75-90×25-25	2-300, D, C, T
1024	Penstemon	26-30×12.5-13×9.5-10.5	95-120×21-25	350-400, D, C, T
1104	Artemisia	26.5-28×11-12.5×9-10.5	90-106×23-25	250-350, D, C, T
1132a	Carum	26.5-30×12-14×9-10.5	88-115×23-25	300, D, C, T
1028	Cynomorathrum	26.5-32×9-12.5×9	88-106×26.5-30	150-300, D, C, T
B				
1026a	Umbellifer	30-40×16-21×11-14	125-160×26-30	250-350, D, C
1134a	Linum	38-43×19-24×12.5-15	160-175×35-40	350-550, d, T

section A, although showing quite a bit of difference in spore size, are all very similar and are placed in *P. permunda*.

In Table 5 are listed the collections with 4- or 5-septate spores. Section A includes the 4-septate collections which show a continuous series and are placed under *P. aurea*. The single collection in Section B has a spore form different from all the other clathrate spores seen and seems to be a new species. The collection in Section C has the same spore form as those previously mentioned but the spores are 5-septate. It is the same as *P. planispora* Ellis.

#### PLEOSPORA (CLATHROSPORA) PERMUNDA (Cke.) Sacc.

Pl. 3, Figs. 30-31

Perithecia thickly and widely scattered beneath the epidermis, tardily superficial by the exfoliation of this tissue, flattened-spheric, disc-like with

a minute central ostiole, 200–400 $\mu$  in diameter, soon collapsing pezizoid, saucer shaped with age and surrounded by a more or less dense halo of dark brown septate radiating hyphae which is commonly visible through the epidermis and quite characteristic.

Asci broadly clavate, with a thickened wall and a claw-like base, 75–115×19–30 $\mu$ .

Spores biseriate, broadly rhomboid-fusoid to clavate-ellipsoid in face view, 3-septate, end cross walls often at an oblique "Y" angle to the single central septum which is found in two central cells but not in the end cells;

TABLE 5. *Spores clathrate, 4- to 5-septate*

No.	Host	Spore Range	Septa-tion	Asci	Perithecia
A					
1129b	Delphinium	23–28×11–11.5×8–10	4	85–90×21–25	2–250, D, c, T
1110d	Lupinus	26–30×12–13×8–9	4	88–97×23–26	250–350, D
1130a	Lupinus	26–32×11–13×8–10	4	85–90×18–21	250–350, D, C, T
1131b	Clematis	26.5–30×11–12×7.5–8	4	95–115×21–23	250–350, D, C, T
B					
1101d	Lupinus	23.5–28.5×9–11×7–8.5	5	100–125×12–16	3–400, D, C
C					
1201d	Penstemon	28–35×13–16×9–11	5	78–100×23–26	300, d, t

cylindric to fusoid or inaequilateral in edge view, with no vertical walls visible, 21–32×10–12.5 (14)×7–10 $\mu$ .

Camp Davis: on *Penstemon glaber* Pursh, June 18 (1016b); and *P. stenosepalus* (A. Gray) Howell, July 5 (1086a).

Cream Puff Mt: on *Penstemon stenosepalus* (A. Gray) Howell, July 5 (1086a).

Gros Ventre River: on *Stephanomeria tenuifolia* (Torr.) Hall, July 19 (1158).

Glory Mt.: June 20, on *Syntheris dissecta* Rydb. (1032); *Penstemon* sp. (1024); *Linaria vulgaris* Mill. (1023b); *Balsamorrhiza sagittata* (1025); and *Cynomarathrum Parryi* (S. Wats.) Coulter & Rose (1028).

South of Teton Pass: July 11, on *Lupinus parviflorus* Nutt. (1110c); *Sambucus microbotrys* Rydb. (1133b); *Delphinium Brownii* Rydb. (1129a); *Clematis Douglasii* Hook. (1124b); *Hedysarum uintahensis* A. Nels. (1126b); *Lupinus parviflorus* Nutt. (1110c & 1130b); *Carum Carui* L. (1132a); *Valeriana* sp. (1128a); and *Linum Lewisii* Pursh (1134f).

Togwotee Pass: July 8, on *Helianthella* (?) (1100a); and *Artemisia pedatifida* Nutt. (1104).

Skyline Trail: Death Canyon, on *Brickellia grandiflora* Nutt., Aug. 4,

(1209); Overlook, on *Senecio sp.*, Aug. 4 (1208b) and on *Carum Carui* L., July 24 (1166a).

This is the most common of all the species of *Pleospora* in this region of Wyoming. It was found on a wide range of hosts, often mixed in with other fungi and probably could be isolated from other collections if looked for intensively. It is quite distinct, when plentiful, having small collapsing cup-shaped perithecia with a halo of tomentum easily distinguishable under a lens.

As seen in Table 4, section A, these collections show a continuous overlapping series of spore lengths from 21 to 31 $\mu$ . Cooke's description of *Sphaeria permunda* in Vize (9, p. 111) is an incomplete one and gives the spores as  $30 \times 15\mu$ . Ellis (4, p. 341) gives the spores as  $20-24 \times 10-11\mu$ , whereas Berlese (2, 2; 29) says that spores from an Ellis specimen measure  $23-26 \times 12-15 \times 8\mu$ . Berlese's figures (2, 2, Pl. 45, fig. 1) are typical of these western species. There is evidence that certain extremes of this series, as well as certain other variations might be separated as varieties, but further data in support of this evidence is needed before one can be confident that these do reoccur as good varieties.

On *Cynomarathrum*, the spores are mostly immature, are more tapered toward one end and are commonly without vertical septa in some of the central cells. Decision as to whether this is a good variety or merely a young condition depends upon comparison with further collections.

#### PLEOSPORA (CLATHROSPORA) DIPLOSPORA E. & E.

Pl. 3, Fig. 32

Perithecia scattered, somewhat depressed-spheric, 250–600 $\mu$  in diameter, not collapsing but with a radiating basal tomentum of rather stiff, unbranched, brown hairs.

Asci clavate, thick-walled, with a claw-like base,  $125-175 \times 26-40\mu$ .

Spores biseriate, ovoid, rhomboid-ellipsoid, clathrate-flattened, 3-septate, central cells with a vertical septum, end cells without vertical walls, cylindric to fusoid in edge view, without any vertical walls,  $30-43 \times 16-24 \times 12.5-15\mu$ .

Glory Mt. on umbellifer, June 20 (1026a).

South of Teton Pass: on *Linum Lewisii* Pursh, July 11 (1134a).

The two collections in section B of Table 4 have spores identical with those in section A but show an extension in the size range. Ellis (5, p. 20) described *Pleospora diplospora*, on *Asclepias*, as having clathrate spores,  $24-30 \times 10-15 \times 7-8\mu$ , which were at first 3- then 5- to 7-septate. Berlese (2, 2; 30) states that material sent him by Ellis is a mixture of *Pleospora herbarum* (with 5- to 7-septate spores) and a clathrate species with 3-septate spores, which he renames *Clathrospora Ellisiiana* Berl. He gives the spores as  $32-35 \times 16-18 \times 12\mu$ . The type of *P. diplospora* (N. Y. B. Gard.,

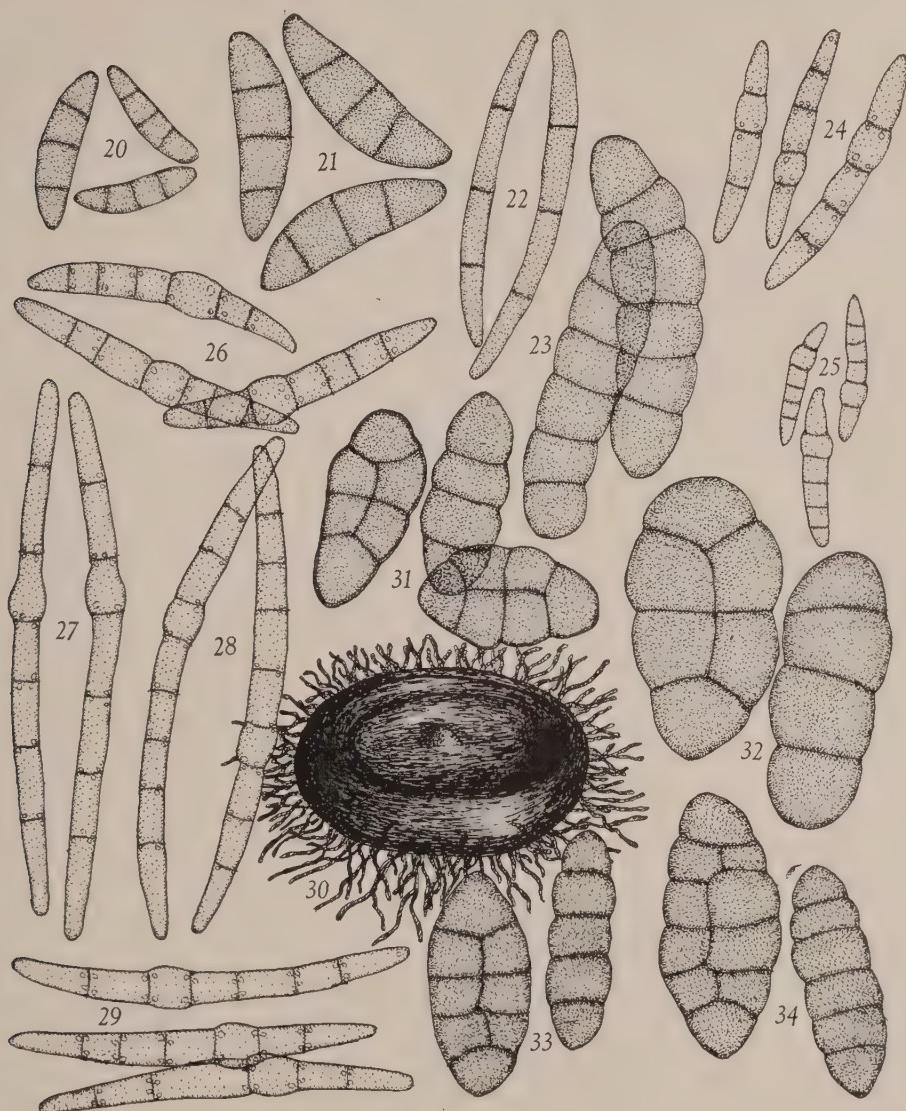


PLATE 3. 20. *Leptosphaeria eustoma* (Fr.) Sacc. sensu Berl. 21. *Leptosphaeria Euphorbiae* Niessl. 22. *Leptosphaeria tetonensis* sp. nov. 23. *Leptosphaeria* sp., from *Agastache*. 24. *Leptosphaeria oreophila* Sacc. 25. *Leptosphaeria tenera* Ellis. 26. *Leptosphaeria agnita* (Desm.) Ces. & de Not. 27. *Leptosphaeria olivacea* Ellis. 28. *Leptosphaeria octoseptata* sp. nov. 29. *Leptosphaeria Erigerontis* Berl. 30. Perithecioid of *Pleospora (Clathrospora) permunda*, of the tomentose collapsed type, common to many species of the clathrate *Pleosporae*. 31. *Pleospora (Clathrospora) permunda* (Cke.) Sacc. 32. *Pleospora (Clathrospora) diplospora* E. & E. 33. *Pleospora (Clathrospora) aurea* Ellis. 34. *Pleospora (Clathrospora) planispora* Ellis. Scale, 1 mm. = 1 $\mu$ . Figs. 20-29, 31-34. Ascospores.

Ell. coll. No. 894) includes drawings of these 5- to 7-septate spores and states that they come from the same perithecia as the 3-septate ones. Examination of the material shows that the many septate spores are only on the surface. They are abnormal and seem to be germination stages of the 3-septate spores, having a variable number of transverse, but always one central vertical septum. They do not belong to *P. herbarum*, and there is no reason for changing Ellis' name, inasmuch as it is quite obvious that he is describing the 3-septate clathrate species which is present and which has spores  $30-35 \times 14-19 \times 8.5-10.5\mu$  in the type material. Several species of Pleospora are commonly found mixed on type material, and this is no reason for a name change. The species must be interpreted through the original description, where possible.

PLEOSPORA (CLATHROSPORA) AUREA Ellis

Pl. 3, Fig. 33

Perithecia widely or thickly scattered,  $200-350\mu$  in diameter, depressed-spheric, collapsing pezizoid with age, with a basal halo of radiating, dark brown, hyphal tomentum, usually visible through the epidermis, beneath which the perithecia are imbedded.

Asci clavate, thick-walled, with a claw-like base,  $85-115 \times 18-26\mu$ .

Spores biseriate, rhomboid to ovoid in face view, flattened, 4-septate, with vertical septa in the central but not in the end cells, end cross-walls often bent at an angle where they meet the vertical septum, oblong to fusoid-ellipsoid in edge view, without any vertical septum visible,  $26-32 \times 11-14 \times 7.5-10\mu$ .

South of Teton Pass: July 11, on *Delphinium Brounii* Rydb. (1129b); *Lupinus parviflorus* Nutt. (1110d & 1130a); and *Clematis Douglassi* Hook. (1131b).

Section A, in Table 5, represents the 4-septate spore group of the clathrate series. Here, again, there are overlapping spore sizes running from 23 to  $32\mu$  in length, giving a series parallel to that of *P. permunda* but differing in the extra septum. All of the Wyoming collections were taken in one locality, but on different hosts.

There are six species, *P. platyspora* Sacc., *P. quadriseptata* Cke. & Harkn. *P. pentamera* Karst., *P. aurea* Ell., *P. Passeriniana* Berl., and *P. Pteridis* Lind, described with 4-septate spores of this type. It is possible that some of these species represent varietal sections of the rather wide spore range shown here, but an examination of the literature shows that each species has been interpreted differently and given different spore ranges by different authors. Finally, Lind (7, p. 165) has placed all but *P. quadriseptata* in synonymy under *P. pentamera*. His figures of this species, from Nova Zembla (6, Pl. 2, fig. 2) shows spores which are more ellipsoid, or clavate than the rhomboid spores of the Wyoming collections. Inasmuch as there

may be variations in this series which should later be segregated, the binomial *P. aurea* is used here instead.

The type of *P. aurea* Ellis (N. Y. B. Gard., Ellis coll., 1881) has spores which are typical of the Wyoming collections, and  $23-26.5 \times 10.5-12.5 \times 7-9\mu$ , which is in the lower range of this series. Furthermore, a second packet (collected in 1882), with the type, shows spores  $27-32 \times 12-12.5 \times 7-9\mu$ , which lie in the upper range as represented in section A.

### PLEOSPORA (CLATHROSPORA) PLANISPORA Ellis

Pl. 3, Fig. 34

Perithecia scattered, somewhat depressed-globose, slightly tomentose at the base, about  $300\mu$  in diameter.

Asci clavate, thick-walled, with a claw-like base,  $78-100\mu \times 23-26\mu$ .

Spores biseriate, broadly rhomboid- to fusoid-ellipsoid in face view, flattened, 5-septate, not constricted at the septa, with a single vertical septum passing through the central cells, commonly with a characteristic "jog" where it crosses the 2nd and 4th septum, without vertical walls in the end cells, cylindric to fusoid-ellipsoid in edge view with no vertical septa visible,  $28-35 \times 13-16 \times 9-11\mu$ .

Camp Davis: on *Penstemon glaber* Pursh, Aug. 3 (1201d).

The single collection of this species represents the continuation of the tendency towards an increase in the number of septa formed in this clathrate series. The type of *P. planispora* (N. Y. B. Gard., Ellis coll., Harkness No. 94), which is distributed in N. A. F. No. 1584, is a mixture of a 4-septate and a 5-septate, clathrate Pleospora. In Ellis' manuscript description he gives the spores as 4- to 5-septate, but in the published description they are given only as 5-septate. The two species seem to be distinct. The 5-septate spores (fig. 34) are  $28-41 \times 13-17 \times 8-10\mu$  and differ from the 4-septate ones in the fainter septa and the characteristic "jog" where the 2nd and 4th septa cross the vertical wall.

### Pleospora (Clathrospora) togwotiensis sp. nov.

Pl. 1, Fig. 12

Scattered as black circular spots which are the depressed-spheric perithecia,  $300-400\mu$  in diameter, immersed beneath the epidermis. Perithecia collapsing pezizoid, with a minute central papillate ostiole but no basal tomentum. Walls of coarse dark parenchyma.

Asci long cylindric, with a thickened wall and a claw-like base,  $100-125 \times 12-16\mu$ .

Spores overlapping, uniseriate, flattened, muriform, narrowly fusoid-ellipsoid, inaequilateral or slightly curved in face view, 5-septate, with one vertical septum in each cell except the end cells, constricted at the septa,

cylindric to fusoid-cylindric in edge view, with no visible vertical walls,  $23.5-28.5 \times 9-11 \times 7-8.5\mu$ .

Togwotee Pass: on *Lupinus candidans* Rydb., July 8 (1101d) (Type).

Perithecia nigra maculiformia, depresso sphaerica, sub epidermate in caulis *Lupini candidantis* Rydb. dispersa,  $300-400\mu$  diametro, demum delapsu cupuliformia; ostiolo centrali, minuto, papilliforme praedita, absque tomento basali; pariete fusco ex parenchymate crasso constante. Ascii longe cylindrici, basi unguiculiformes,  $100-125\mu$  longi,  $12-16\mu$  crassi, membrana crassa. Sporae uniseriatae, imbricatae, applanate muriformes, 5-septatae, ad septa constrictae,  $23.5-28.5\mu$  longae,  $9-11\mu$  latae,  $7-8.5\mu$  crassae, in aspectu frontaliam anguste fusoideo-ellipsoidales, inaequilaterales vel paulum curvatae, cum cellulis centralibus verticaliter uniseptatae (omnibus, apicalibus exceptis), in aspectu laterali cylindricae vel fusoideo-cylindricae, absque septis visibilibus.

Specimen typicum in caulis vetustis *Lupini candidantis* Rydb., ad locum dictum Breccia Peak, prope Togwotee Pass, Teton Co., Wyoming, 8 Jul., 1940, legit L. E. Wehmeyer, sub numero 1101d.

This single collection differs from all of the other collections with clathrate spores in the narrowly ellipsoid spore form and the definite constrictions at the septa. The ascii are also longer and narrower.

It resembles *Clathrospora Donacis* Berl. somewhat, in these characters, but that species is figured by Berlese (2, p. 48, fig. 2) as having two vertical septa, whereas this collection has only one.

#### LEPTOSPHAERIA

The taxonomic situation in Leptosphaeria is much the same as it is in Pleospora. The spore forms can also be derived from the same type of 3-septate dark brown spore, but in this genus a different course in the evolution of the spore and ascus has occurred. The spores tend to become lighter in color, more elongate, narrower, and more septate. This tendency leads directly, without a break, into the genus Ophiobolus. In one series, there is a definite tendency for one of the cells of the spore to become somewhat enlarged or swollen. The number of septa and the position of this swollen cell seem to be quite constant.

The ascii in Leptosphaeria tend to become narrowly clavate with only a slight thickening in the apical wall. The more elongated spores tend to become arranged in a parallel fascicle, and at maturity the base of the ascus becomes elongate attenuate. A pressure is generated in the upper portion of the ascus, which apparently ruptures the weakened basal portion of the ascus, and squeezes the spores out through the lower end.

The perithecia in Leptosphaeria tend to be more permanently immersed and occur in more "pure stands," and not mixed with other fungi as those of Pleospora often are. They are rarely of the collapsed, pezizoid type so commonly found in Pleospora, but may be tomentose.

There are some 382 species of Leptosphaeria described with the simple 3-septate type of ascospore. Many of these must obviously be synonyms, but the great number of names indicates the plentifullness of this type.

Comparatively, only a few of this type were found among the Wyoming collections.

LEPTOSPHAERIA EUSTOMA (Fr.) Sacc. Sensu Berl.

Pl. 3, Fig. 20

Perithecia scattered or clustered, small,  $90-150\text{ (200)}\mu$  in diameter, formed beneath the epidermis which is ruptured and thrown off, globose at first becoming depressed and pezizoid collapsed, sometimes with a sparse radiating tomentum at the base.

Asci broad- to narrow-clavate, wall somewhat thickened, with a claw-like base, not tapered below,  $45-70\times 8-12\mu$ .

Spores biseriate, fusoid-ellipsoid, inaequilateral to curved, deep yellow-brown, 3-septate, not much constricted at the septum,  $16-20\text{ (23)}\times 3.5-5.3\mu$ .

Hoback Canyon: on *Draba luteola* Greene (Red Creek), July 29 (1185).

South of Teton Pass: July 11, on *Thalictrum occidentale* Gray (1115a); and *Aquilegia coerulea* James (1114a).

The collections on *Thalictrum* and *Aquilegia* are very similar; the one on *Draba* differs somewhat in the broader asci ( $45-70\times 9-12$ ) and larger spores ( $16-23\times 4.3-5.3\mu$ ) which are somewhat more constricted, and the small perithecia ( $90-140\mu$ ) which are not collapsed, but these differences do not seem sufficient for a separate species, at least until more material so indicates.

There are a score of more species of *Leptosphaeria* described with small perithecia and 3-septate spores within this size range. Only a comparative study of a large number of collections of these species can determine what if any are good lines of specific demarcation. Berlese (2, 1; 55) has placed a large number of these as forms of *L. eustoma* (Fr.) Sacc., the spores of which he gives as  $17-20\times 4-5\mu$ . Consequently, these collections are referred to *L. eustoma*, in the sense of Berlese, as a collective species, until such time as differential characters can be established.

LEPTOSPHAERIA EUPHORBIAE Niessl (?)

Pl. 3, Fig. 21

Perithecia scattered or clustered, small,  $150-200\mu$  in diameter, sphaeric or slightly flattened, with a slight growth of tomentum at the base.

Asci stout clavate, rather thick-walled, with a claw-like base,  $70-78\times 17-18\mu$ .

Spores overlapping biseriate, fusoid-ellipsoid, inaequilateral to slightly curved, 3-septate, dark yellow-brown, not constricted at the septa,  $25-30\times 7-8\mu$ .

Skyline Trail: on *Carum Carui* L., July 24, (1166c).

This species differs from the last chiefly in the larger, broader spores.

As in the case of the previous species, there are a large number of species described in this general spore range. This collection differs from *L. Doliolum* in the larger, biseriate spores and broader ascii. It comes closer to *L. vagabunda* in its ascus characters, but the spores in that species are smaller, again. *L. Steironematis* Ell. is also similar but has shorter and broader spores and the type shows much larger perithecia,  $300\text{--}600\mu$  in diameter. The description of *L. Euphorbiae* Niessl seems to fit better than any other.

✓ **Leptosphaeria tetonensis** sp. nov.

Pl. 3, Fig. 22

Perithecia globose to somewhat depressed,  $200\text{--}300\mu$  in diameter, thickly scattered and formed beneath the epidermis, but superficial and shiny black on old stems, ostiole fairly prominent, papillate to short cylindric, walls about  $30\mu$  thick, of dark walled parenchyma.

Asci clavate, with a thickened apical wall and a claw-like base, becoming attenuate below,  $78\text{--}90 \times 12\text{--}13\mu$ . Paraphysis-like strips of interthelial tissue present between the asci.

Spores overlapping 3-seriate, elongately fusoid-cylindric, straight or curved, 3-septate, pale yellow-brown, not constricted at the septa,  $44\text{--}48 \times 3.5\text{--}4\mu$ .

South of Teton Pass: on *Pedicularis bracteosa* Benth., July 11 (1117) (Type).

Perithecia globosa vel paulum depressa,  $200\text{--}300\mu$  diametro, dense dispersa, primum sub epidermate sed ultimo in caulis vetustis superficialia, atra, nitida; ostiolo modice prominenti, papilliformi vel breviter cylindrico; pariete ca.  $30\mu$  crasso, atro, parenchymatoso; ascis clavatis,  $78\text{--}90\mu$  longis,  $12\text{--}13\mu$  crassis, ad apicem pariete incrassatis, basi unguiformibus demum attenuatis, separatis a pseudoparaphysibus; sporis  $44\text{--}48\mu$  longis,  $3.5\text{--}4\mu$  crassis, triseriatis, imbricatis longe fusiformiter cylindricis, rectis vel curvatis, 3-septatis, pallide lutei-brunneis, ad septa non constrictis.

Specimen typicum in caulis vetustis *Pedicularis bracteosa* Benth., prope "Teton Pass," Jackson, Wyoming, 11 Jul., 1940, legit L. E. Wehmeyer, sub numero 1117.

This species is distinctive among those with 3-septate spores in the long narrow, non constricted spores. It is very similar to *L. petkovicensis*, but that species has smaller perithecia ( $100\text{--}200\mu$ ) and occurs on *Juncus*, which indicates it is probably distinct.

A Septoria with long needle-like spores  $40\text{--}45 \times 1\text{--}1.5\mu$  occurs abundantly on these same stems.

**LEPTOSPHAERIA** sp.

Pl. 3, Fig. 23

Perithecia scattered. Ascii broad-clavate, thick-walled, base claw-like,  $85\text{--}106 \times 28\text{--}31\mu$ .

Spores biseriate, fusoid to cylindric, straight to somewhat curved, dark brown, 5- or rarely 6-septate, constricted at first at the central septum, later at all the septa,  $31\text{--}44 \times 10.5\text{--}12.5\mu$ .

TABLE 6

No.	Host	Spore Range	Septation	Asci	Perithecia
A					
1035	Pedicularis	(23) 26-34×3.5-4	4	70-80×8.5-10.5	2-250, d
1126c	Hedysarum	25-28.5×3.5-4	4		250-300, d
1022a	Umbellifer	26-32×3.5	4	78-90×9-11	2-300, G, d
1197	Boykinia	26.5-31×3.5	4		150-200
1045	Delphinium	27-30×3.5-4	4	60-70×8.5-10.5	250-300, D
1159b	Castilleja	28.5-31×3.5-4	4	60-70×8.5-10	180-250, t
1056a	Aquilegia	32×3.5-4	4	45-70×8-9	200
B					
1131d	Clematis	18-23×2.5-3.5	5	75-95×6-7	2-350, G
C					
1065	Lupinus	35-39×3.5-4.5	6	70-90×9-12	2-300, d
1043a	Castilleja	35-40×3.5-4	6	78-90×9-12	2-250, d
1110e	Lupinus	39-42×4-4.5	6	88-97×12.5	2-350, g
1130	Lupinus	39-45 (47)×4-5.5	6	115-150×12.5	250-350, d
D					
1166b	Carum	(46) 53-60×5-5.5	6	70-80×10-11	300, g, T
1112e	Carum	(48) 53-60×5-5.5	6	88-97×14-15	250-350, d
1111	Heracleum	(49) 53-59×3.5-5	6	85-115×12.4-14	250-300, d, T
1169	Aconitum	53-57×4.3-5	6	85-90×12.5	2-300, d, T
1114c	Aquilegia	53-60×4.3-5.3	6	100-110×14-16	250, d
1113a	Erigeron	53-60×5	6	97-106×12.5-16	350-400, t
1129c	Delphinium	58.5×3.5	6	100-110×12.5-14	250-350, d, T
E					
1084a	Umbellifer	(60) 67-73×3.5-4	6	90-110×13-14	2-275, d
1112	Carum	67-74×4.5-5	6	90-150×14	2-300, d
1109b	Agastache	67.5-74×4.5-5	6	90-105×14	2-250, d
1026b	Umbellifer	(56) 69-75×4-4.5	6	85-95×12-16	2-250, d
1132	Carum	70-74×5	6	96×105×15	3-350, g
F					
1168	Senecio	66-78×3.5-5	8	85-90 (140)×14-16	3-400, g, T

South of Teton Pass: on *Agastache urticifolia* (Benth.) Rydb., July 11 (1121b).

Only a single perithecium of this species was found, mixed in with many other fungi, and it needs confirmation. There seems to be no other species with these large cylindric dark-brown, 5-septate spores, but inasmuch as insufficient type material is available, no species name is applied at this time.

#### THE "AGNITA" SERIES

Table 6 deals with a series of collections, all of which have spores containing a swollen cell near one end. Most of these collections form an almost

continuous series, but with more definite breaks than in some of the series of *Pleospora*. Section A includes all of the 4-septate spores with a second cell swollen, which appear to be a single species, *L. oreophila* Sacc. The single collection in section B has 5-septate spores which are distinctly smaller, and is *L. tenera* Ell.

Sections C, D, & E, all have 6-septate spores with the third cell somewhat enlarged. There are certain minor differences of form correlated with the increase in spore size here, however, and three species can be distinguished which are placed under *L. agnita* (Desm.) Ces & deNot., *L. Eri-geronitis* Berl. & *L. olivacea* Ell. The spores of these three species are easily confused, however, when only single collections are considered. The collection on *Senecio*, in Section F, is a continuation of this same series with an additional septum inserted on each side of the swollen cell.

#### LEPTOSPHAERIA OREOPHILA Sacc.

Pl. 3, Fig. 24

Perithecia 150–300 $\mu$  in diameter, globose to somewhat depressed-spheric, thickly scattered beneath the epidermis, with a papillate or slightly elongate ostiole erumpent through this tissue, wall parenchymatic, variable in thickness (10–50 $\mu$ ) and often with a slight basal radiating tomentum.

Asci clavate, with a tapering lower portion, and a claw-like basal attachment, wall thickened, particularly above, 60–90×8–11 $\mu$ .

Spores 2- to 3-seriate, fusoid-cylindric, straight or slightly curved, pale yellow-brown, 4-septate, with 2–several small droplets on either side of each septum, second cell somewhat enlarged, 26–34×3.5–4 $\mu$ .

Camp Davis: on *Delphinium Brownii* Rydb., June 24 (1045).

Hoback-Snake River Junction: on *Castilleja linariaefolia* Benth., July 15 (1159b).

Hoback Forest Camp: on *Aquilegia coerulea* James, June 25 (1056a)

Granite Creek Canyon: *Boykinia Jamesii* (Torr.) Engler, Aug. 1 (1197).

South of Teton Pass: June 20, on *Pedicularis bracteosa* Benth. (1035); *Hedysarum uintahense* A. Nels., (1126c) and an umbellifer (1022a).

The small droplets lying on each side of the septa, even before these septa themselves are apparent, are typical of the spores of this series.

These collections belong to a group of species including *L. oreophila* Sacc. *L. Niessleana* Rab., *L. quadrisepata* Trail, *L. Lonchampsii* (West.) Sacc., *L. primulana* All., *L. montana* Trav. and *L. spectabilis* Niessl (sensu Berl.). The spore range in one mount will cover that given for all these species. *L. oreophila* is merely chosen as the earliest binomial with the most suitable description.

## LEPTOSPHAERIA TENERA Ellis

Pl. 3, Fig. 25

Perithecia somewhat depressed-globose,  $200\text{--}350\mu$  in diameter, formed beneath the epidermis, but this tissue later exfoliated, erumpent at first as a minute papillate ostiole, usually thickly scattered, wall membranous,  $20\mu$  thick.

Asci clavate, wall somewhat thickened, base claw-like, becoming long tapered below and breaking away allowing the spores to escape from the lower end,  $75\text{--}95 \times 6\text{--}7\mu$ .

Spores 2- to 3-seriate, fusoid-cylindric, straight or slightly curved, pale yellow, 5-septate, second cell somewhat enlarged,  $18\text{--}23 \times 2.5\text{--}3.5\mu$ .

South of Teton Pass: on *Clematis Douglasi* Hook., July 11 (1131d).

The type (N. Y. B. Gard., Ellis coll., Harkness No. 3) of *L. tenera* is identical with this collection, although the spores are slightly paler, probably because they are not so mature. Although having an additional septum, these spores are smaller than those of *L. oreophila*.

## LEPTOSPHAERIA AGNITA (Desm.) Ces. &amp; deNot.

Pl. 3, Fig. 26

Perithecia scattered over wide areas of the stems, which are not much discolored, causing papillate pustules and erumpent as minute papillate ostioles,  $200\text{--}300\mu$  in diameter, globose or slightly depressed, walls  $20\text{--}30\mu$  thick, composed of dark colored parenchyma.

Asci short clavate at first, with a thickened apical wall and a claw-like base, basal portion becoming elongate and tapered,  $70\text{--}115 (150) \times 9\text{--}12.5\mu$ .

Spores fasciculate, parallel at first, slipping over one another as the ascus elongates, fusoid-cylindric, pale yellow-brown, 6-septate, constricted at first at the 3rd septum, which is practically in the middle of the spore, third cell becoming enlarged. Spores tapered equally toward both ends, with droplets on each side of each septum, somewhat curved,  $35\text{--}45 (47) \times 3.5\text{--}5.5\mu$ .

Camp Davis: on *Castilleja miniata* Dougl., June 24 (1043a); and *Lupinus parviflorus* Nutt., June 26 (1065).

South of Teton Pass: on *Lupinus parviflorus* Nutt., July 11 (1110e & 1130).

Berlese's figures (2, 1; 81, Pl. 71, fig. 1) and spore measurements ( $34\text{--}38 \times 4\text{--}5$ ) for *L. agnita* fit this collection very well. *L. acuta* (Moug. & Nestl.) is also very similar. This species differs from the following two in the shorter spores and in the position of the constriction at the third septum which is practically in the center of the spore in this species. It seems to favor stems of Lupinus as three of the four collections were on that host.

## LEPTOSPHAERIA ERIGERONTIS Berl.

Pl. 3, Fig. 29

Perithecia  $250\text{--}350\mu$  in diameter, somewhat depressed-globose, thickly scattered in localized, slightly blackened or discolored areas, beneath the epidermis, causing conic pustules with only the papillate ostiole erumpent, often with brown, radiating hyphae about the base beneath the periderm.

Asci short clavate at first, with a thickened apical wall, into which a cylindric extension of the protoplasm extends, base claw-like, becoming attenuated and dissolving to allow the escape of the spores,  $70\text{--}115 \times 12.5\text{--}15\mu$ .

Spores parallel in the ascus at first, then 4-seriate, elongately cylindric-fusoid, 6-septate, somewhat curved, evenly tapered toward the ends, with the third cell somewhat enlarged, pale yellow-brown, with small globules on each side of the septa (46)  $53\text{--}60 \times 3.5\text{--}5.5\mu$ .

South of Teton Pass: July 11, on *Carum Carui L.* (1112e); *Heracleum* sp. (1111); *Delphinium Brownii* Rydb., (1129c); *Erigeron salsuginosus* (Rich.) A. Gray (1113a); and *Aquilegia coerulea* James (1114c).

Skyline Trail: on *Carum Carui L.*, July 24 (1166b).

There is doubt as to just what *L. Erigerontis* is. It was first described by Berlese (1) as a variety of *L. agnita* from material sent by Ellis on *Erigeron canadensis*. He gave the spores as  $48\text{--}50 \times 4\text{--}5\mu$  and his figure (2, 1, Pl. 71, fig. 3) shows a spore similar to that described for *L. agnita*, with the constriction practically in the middle, but the spore measurements agree better with this group of collections. Collections of this species in the N. Y. Bot. Garden show a variety of four or five different Leptosphaerias. An Ellis collection, on *Lactuca*, labelled *L. agnita* var. *Erigerontis*, has spores  $34\text{--}37 \times 3\text{--}3.5\mu$  which are of the *L. ogilviensis* type with a different shape. The binomial *L. Erigerontis* is used here provisionally.

This species seems to favor the Umbelliferae, since three of the six collections are on umbelliferous hosts. It is easily confused with the following species, *L. olivacea*, particularly, because the two may occur mixed on the same stems (i.e., 1112 & 1112x). *L. Erigerontis* differs in the shorter spores which taper toward the two ends, whereas in *L. olivacea* the spores are more evenly cylindric and the swollen cell is more prominent. *L. Erigerontis* differs from *L. agnita* in the position of the constriction, at the third septum, which in the former is above the middle of the spore.

## LEPTOSPHAERIA OLIVACEA Ellis

Pl. 3, Fig. 27

Perithecia globose to slightly depressed,  $200\text{--}400\mu$  in diameter, thickly scattered beneath the epidermis in locally blackened or somewhat discolored areas, forming small conic pustules, and erumpent as small papillate ostioles, walls  $20\text{--}40\mu$  thick, of rather small, dark-walled parenchyma.

Asci clavate, soon with an elongate tapered base, apical wall thickened and often with a cylindric extension of protoplasm projecting into it,  $70-110 \times 13-16\mu$ , or up to  $160\mu$ , as the base elongates at spore ejection.

Spores 4-seriate to overlapping fasciculate, elongately cylindric-fusoid, pale yellow-brown, somewhat curved, 6-septate, at first constricted at the third septum and then with the third cell somewhat enlarged, ends of spores rounded, not much tapered, with small globules on each side of the septa (60)  $67-75 \times 3.5-5\mu$ .

Cream Puff Mt.: On Umbellifer stems, July 5 (1084a).

Glory Mt.: on Umbellifer stems, June 20 (1026b).

South of Teton Pass: July 11, on *Carum Carui* L. (1112 & 1132); and *Agastache urticifolia* (Benth.) Rydb. (1109b).

Ellis (3, p. 53) described *L. olivacea*, from herbaceous stems, from Utah. He gave the spores as  $75 \times 3.5\mu$ , 6- to 7-septate, and with the third cell swollen. His figure (4, Pl. 28, fig. 13) shows its spore as of the same type as in these collections, but 7-septate. Berlese and Voglino (in Saccardo, Add. Fung. Syll. 186) placed this species in *Ophiobolus*. Whatever the line of demarcation is to be between *Leptosphaeria* and *Ophiobolus*, it will have to be purely arbitrary. Inasmuch as this species is obviously closely related to the two preceding, it is retained in *Leptosphaeria*.

This species differs from *L. Erigerontis*, as here interpreted, in the longer spores and the sudden narrowing of the swollen cell, with the remainder of the spore length being cylindric with very little taper, rather than gradually tapering toward the end, as in that species. It, again, seems to favor the stems of umbellifers.

### *Leptosphaeria octoseptata* sp. nov.

Pl. 3, Fig. 28

Perithecia thickly scattered over wide areas of the stem, slightly depressed globose,  $300-400\mu$  in diameter, formed beneath the epidermis, at first erumpent only as the small papillate ostiole, later erumpent-superficial by exfoliation of the epidermis, with a basal radiating tomentum beneath the epidermis and often a tomentum of short hairs over the entire surface.

Asci clavate at first,  $85-90\mu$  long, then with a long tapering base,  $140 \times 14-16\mu$ , apical wall somewhat thickened.

Spores overlapping fasciculate in the ascus, elongately fusoid-cylindric, slightly curved, ends acute, pale yellow, typically 8-septate, fourth cell slightly swollen, small guttulae on each side of the septa,  $66-78 \times 3.5-5\mu$ .

Skyline Trail: on *Senecio crassulus* Gray, July 24, legit L. E. Wehmeyer (No. 1168), (Type).

Perithecia dense dispersa in areis caulis latis, depressiusculae globosa, diametro  $300-400\mu$ , sub epidermate formantia, primum solum erumpentia ut ostiola papilliformia, demum super-

ficialiter erumpentia a epidermatis exfoliatione, tomento basali radiato subepidermali praedita, omnino breviter tomentosa. Ascii juvenales clavati, vetustiores basi angustati,  $140\mu$  longi,  $14-16\mu$  crassi, membrana apicali crassiuscula. Sporae irregulariter fasciculatae, longe fusiformi-cylindricae, paulum curvatae, apicibus acutae, pallide luteae, typice, 8-septatae, guttulis typice utrinque ad latera ambo septorum omnium,  $66-78\mu$  longae,  $3.5-5\mu$  crassae; cellula quarta modice dilatata.

Specimen typicum in caulibus vetustis *Senecionis crassuli*, secus viam "Skyline Trail," Teton National Park, Wyoming, 24 Jul., 1940, legit L. E. Wehmeyer, sub numero 1168.

This species is the culmination of the agnita series, having the spore form of *L. olivacea* but with more acute ends, and showing the insertion of an additional cross wall on each side of the swollen cell, as a result of the elongation of the spore.

A second collection (1065a) on *Lupinus parviflorus*, from Camp Davis, with similar spores  $50-60 \times 2-3\mu$  and showing 7 to 9 faint septa, but no swollen cell, may well be an immature specimen of this species and is referred here for the present. *L. Drabae* (Nyl.) Karst. is the only described species of Leptosphaeria which at all resembles this collection, and its description is insufficient to fix it as the same.

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